AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 157:339–346 (2015)

Brief Communication: Body Mass of Wild Bornean Orangutans Living in Human-Dominated Landscapes: Implications for Understanding Their Ecology and Conservation

Yaya Rayadin[1,2] and Stephanie N. Spehar[3]*

[1]*Ecology and Conservation Center for Tropical Studies (ECOSITROP), Samarinda, East Kalimantan, Indonesia*
[2]*Biodiversity Conservation Laboratory, Forestry Faculty of Mulawarman University, Samarinda 75123, East Kalimantan, Indonesia*
[3]*Anthropology Program, University of Wisconsin Oshkosh, Oshkosh, WI 54901, USA*

KEY WORDS *Pongo pygmaeus morio*; allometry; energetics

ABSTRACT Body mass is a key determinant of a species' ecology, including locomotion, foraging strategies, and energetics. Accurate information on the body mass of wild primates allows us to develop explanatory models for relationships among body size, ecology, and behavior and is crucial for reconstructing the ecology and behavior of fossil primates and hominins. Information on body mass can also provide indirect information on health and can be an important tool for conservation in the context of increasingly widespread habitat disturbance. This study reports body mass data recorded for wild Northeast Bornean orangutans (*Pongo pygmaeus morio*) during relocation efforts in forestry and oil palm plantations in East Kalimantan, Indonesia. The average mass of flanged adult males (n = 12, 74 ± 9.78 kg) and adult females (n = 7, 35.29 ± 7.32 kg) from this study were 13.6% and 9% lower, respectively, than the only other published wild Bornean orangutan body mass measurements, but the range of weights for both males and females was larger for this study. This pattern could be due to sampling error, data collection differences, or the influence of habitat disturbance, specifically a lack of access to resources, on individual health. When necessary relocations present the opportunity, we encourage researchers to prioritize the collection of body size data for the purposes of understanding ecology but also as an indirect means of monitoring population viability. As primate habitat becomes increasingly fragmented and altered by humans such data will become critical to our ability to make informed conservation decisions. Am J Phys Anthropol 157:339–346, 2015. © 2015 Wiley Periodicals, Inc.

Body mass is a key component of a species' biology and an important determinant of aspects of their ecology including locomotion, diet, foraging strategies, and energetics (Kleiber, 1961; Bell, 1971; Clutton-Brock and Harvey, 1977; Calder, 1984; Damuth and MacFadden, 1990). It also has an important influence on social behavior, including reproductive and social strategies (e.g., Mitani, 1989; Knott, 2005). Information on wild primate body mass allows us to develop more accurate explanatory models of relationships among body size, ecology, and behavior. These data are thus crucial for reconstructing the ecology of fossil primates and hominins, including the relationship between body size, brain size, and ecological and behavioral adaptations (e.g., Jungers, 1985; McHenry, 1992, 1994; Ruff et al., 1997; Spocter and Manger, 2007). Information on body mass can also be an important tool for conserving primates in the context of increasingly widespread habitat disturbance and fragmentation (Laurance et al., 2000; Chapman and Peres, 2001). Assessing the impact of disturbance on primate populations and the potential conservation value of degraded landscapes requires information on how such landscapes influence population viability. Since demographic information generally used to measure population viability (e.g., natality, mortality, immigration) are difficult to obtain, recent research has emphasized that more direct measures of health, including body mass, can be used to assess the impact of fragmentation on populations and to monitor population status (Dutton et al., 2003, 2008; Junge and Louis, 2005a, 2005b, 2007; Junge et al., 2008; Irwin et al., 2010; Junge et al., 2011).

The orangutan, which is divided into two species (the Bornean orangutan: *Pongo pygmaeus*, and the Sumatran orangutan: *Pongo abelii*), is the only primarily arboreal great ape and the largest arboreal mammal (MacKinnon, 1974). The unusual combination of large body size and arboreality in orangutans has been hypothesized to be a remnant of terrestriality and predator defense strategies from their evolutionary past (MacKinnon, 1974; Rijksen, 1978; Smith and Pilbeam, 1980) or an adaptation providing the strength to exploit fallback foods such as unripe fruit, inner bark, leaves, and nonleafy vegetation (MacKinnon, 1974; Rodman, 1977; Knott, 1998; Taylor, 2006;

Grant sponsor: Arcus Foundation, University of Wisconsin Oshkosh, ECOSITROP.

*Correspondence to: Stephanie Spehar, Anthropology Program, University of Wisconsin Oshkosh, 800 Algoma Blvd., Oshkosh, WI 54901, USA. E-mail: spehars@uwosh.edu

Received 10 December 2014; accepted 21 January 2015

DOI: 10.1002/ajpa.22709
Published online 13 February 2015 in Wiley Online Library (wileyonlinelibrary.com).

Vogel et al., 2008; Marshall et al., 2009a, 2009b; Vogel et al., 2009; Bastian et al., 2010). An alternative hypothesis suggests that their large body size is an adaptation to environments characterized by the unpredictable availability of high-quality resources, as animals with large body size can take advantage of lower-quality food resources and store more energy for times of food shortage (Wheatley, 1982, 1987; Lindstedt and Boyce, 1985; Knott, 1998). The Dipterocarp forests of Southeast Asia exhibit masting cycles that include extended periods of fruit scarcity, providing a strong selective pressure that could have shaped the large body size of orangutans along with several other unique features of their biology (e.g., relatively solitary lifestyle, exceptionally long interbirth intervals) (Wich et al., 2004; van Noordwijk and van Schaik, 2005; Knott, 2005; Knott et al., 2009). Orangutans thus present an interesting case study for investigating the relationships among body size, energetics, and ecology (Wheatley, 1982). Furthermore, cross-species comparisons of great ape ecology are important for enabling more comprehensive reconstructions of the ecology of extinct primates, including hominins.

Finally, understanding the relationship between indicators of health—such as body mass—and habitat disturbance is especially relevant for Bornean orangutans. Bornean orangutans are classified as endangered as their population has declined by over 50% over the last 60 years (Wich et al., 2008; IUCN, 2014). This sharp decline is attributed primarily to forest loss and fragmentation (Marshall et al., 2006; Meijaard et al., 2012), and currently over 75% of the known distribution of Bornean orangutans falls outside of protected areas (Wich et al., 2012). Forest conversion rates in Borneo are among the highest in the world (Curran et al., 2004; Sodhi et al., 2004; Wich et al., 2012) and the island is increasingly characterized by a complex matrix of plantations, coal mines, logging concessions, and human habitation, interspersed with natural forest fragments of varying size and shape (Wich et al., 2008; Meijaard et al., 2011; Wich et al., 2012). In East Kalimantan, these fragments and the surrounding plantations have been found to harbor substantial populations of orangutans (Meijaard et al., 2010a). Orangutans frequently consume the cambium of young *Acacia mangium* trees and the inner pulp of immature oil palm trees, which often causes conflicts with plantation managers and local people (Meijaard et al., 2011; Ancrenaz et al., 2014). However, orangutans rely heavily on natural forest patches within and surrounding these plantations for resources and as nesting sites; similar patterns have been observed in Sumatran orangutans living in mixed agro-forestry habitat (Campbell-Smith et al., 2010, 2011a, 2011b) and Bornean orangutans living in oil palm plantations in Sabah (Ancrenaz et al., 2014) suggesting that orangutans cannot survive in plantation monocultures alone. Overall, the specifics of habitat use and the ability of these habitats to support viable orangutan populations remains unclear. Measures of health status such as body mass can provide further information about the viability of these orangutan populations and can help determine how such landscapes can be integrated into orangutan conservation.

Despite their relevance to orangutan ecology and conservation, accurate body mass measurements are rare because they are extremely difficult to obtain. The only weights for wild orangutans published to-date were those of Dr. W.L. Abbott, obtained from specimens collected during surveys and expeditions in 1907. These weights were first reported by Lyon (1907, 1908, 1911) and then reanalyzed by Eckhardt (1975). Markham and Groves (1990) re-examined the original specimens and determined that several individuals who were not fully adult had been included in the original sample. They omitted these individuals and added to the sample a single adult Bornean orangutan female weighed by another author (Schultz, 1941). This left them very small samples sizes (Bornean orangutans: $n = 4$ flanged adult males and $n = 5$ adult females; Sumatra orangutans: $n = 1$ flanged adult male and $n = 2$ adult females) upon which their final determination of body mass for wild orangutans was based.

Here we expand this sample by reporting body mass for wild Northeast Bornean orangutans (*Pongo pygmaeus morio*) captured during relocation efforts in plantation landscapes in East Kalimantan, Indonesia. Plantation landscapes are heterogeneous, consisting of planted stands of various ages but also natural forest patches of varying size (5–60 ha) and quality, as plantation companies are required by Indonesian law to leave 10% of concessions forested. Orangutans found in isolated forest patches must sometimes be relocated to larger forest patches or forest preserves. As animals are immobilized during this process, it is possible to obtain body mass measurements that can provide information relevant to ecology and conservation.

METHODS

Study sites

All orangutans weighed for this study were captured between 2006 and 2012 in two landscape types in the Kutai Timur and Kutai Kartanegara districts of East Kalimantan, Indonesia: forestry plantations (FP) and oil palm estates (OP). The FP study area consists of ~200,000 ha of fast-growing *Acacia mangium* and *Eucalyptus spp*. of varying age interspersed with patches of degraded forest. This study area is managed by two companies [PT Surya Hutani Jaya (SRH) and PT Sumalindo Hutani Jaya (SHJ)] and was first cleared for planting in 1993 (Fig. 1). Orangutans were first reported using this area in 1996. The OP study area covers ~20,000 ha and is managed by several companies [PT Telen, PT Sawit Prima Nusantara (SPN), PT Telen Prima Sawit (TPS), PT Gemilang Sejahtera Abadi (GSA), and several concessions owned and managed by local communities] (Fig. 1). These estates were established between 2006 and 2007, and orangutans were first observed eating young palm trees in 2011. Kutai National Park (~200,000 ha) is the only protected area in the region, and may serve as a local source and refuge for orangutan populations in areas near the park (Fig. 1).

Procedure for orangutan capture and relocation

Not all orangutans that use plantations are relocated; most are allowed to range freely by plantation management. However, in recognition of the growing use of these landscapes by orangutans, all plantation companies included in this study have established an Orangutan Rescue Team (ORT) trained in orangutan ecology, behavior, and relocation by Dr. Yaya Rayadin, who has over 10 years of experience working with orangutans. When orangutans are observed in situations that pose a danger to their safety or that of human inhabitants, Dr. Rayadin and the ORTs make a decision about relocation.

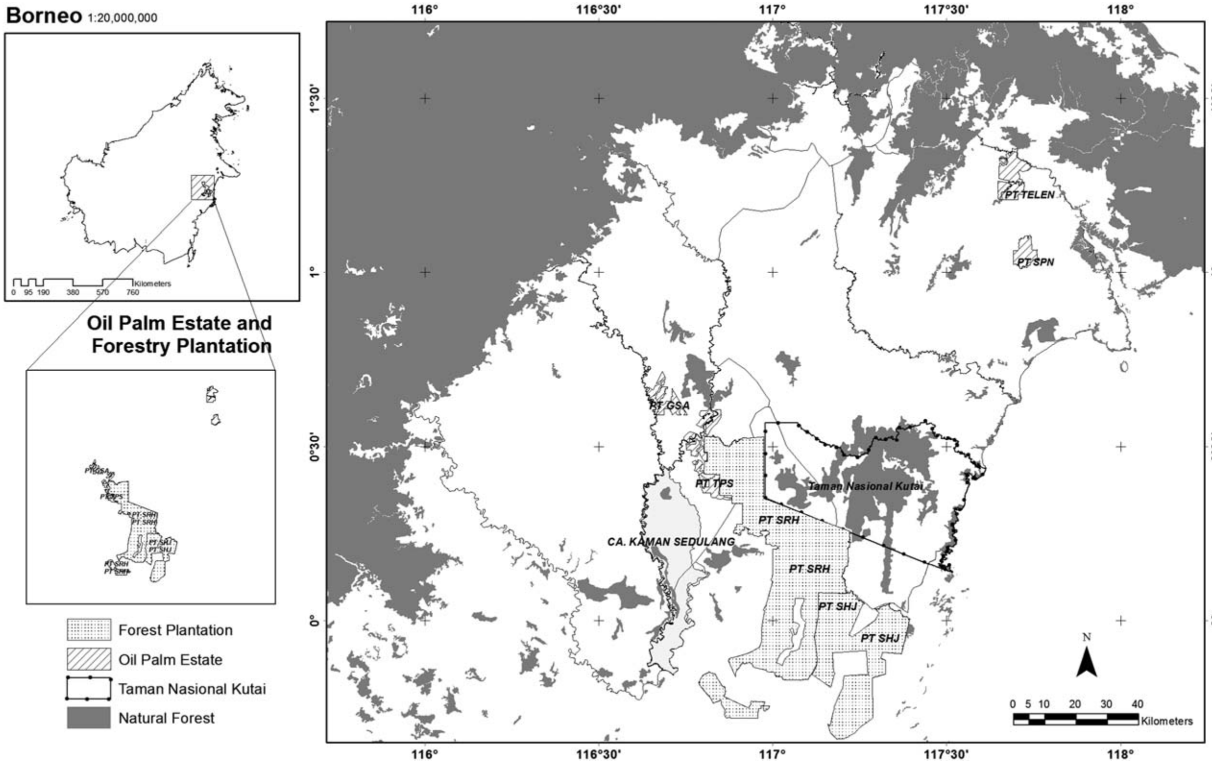

Fig. 1. Location of study sites (forestry plantations and oil palm estates) and Kutai National Park in East Kalimantan, Indonesia.

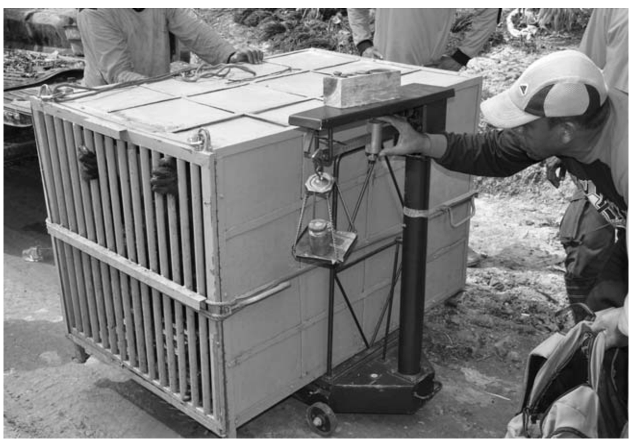

Fig. 2. Obtaining body mass data from captured orangutan.

Variables considered include forest cover, connectivity, patch size, distance from nearest natural forest patch, and other factors that might influence the likelihood of conflict with humans (distance to nearest village, offices, or staff habitation). Relocation is always the last resort and is only done when there are no viable alternatives.

If an orangutan must be relocated, a team consisting of the ORT plus Dr. Rayadin, one veterinarian, three paramedics, and two staff from BKSDA (the local conservation authority) is dispatched. The orangutan is cornered in a low place in the trees and darted using appropriate dosage of 10% Ketamin and 10% Xylazin (Indonesia Law: Permenhut No 48/2008 and Permenhut No 53/2014). The team assembles beneath the orangutan with a sheet, catches the orangutan after the anesthesia takes effect, and transfers the orangutan to a cage. Mothers and infants are placed in separate cages to prevent injury to both parties. While the animal is immobilized an assessment of age-sex class is performed and the individual is weighed (Fig. 2). If the individual is captured before 1,400 h they are immediately taken to a release site (the nearest forested area >30,000 ha in size) and released that same day after behavioral observations indicated they have recovered from the anesthesia. If the individual is captured after 1,400 h they are held overnight and released the following morning.

Data collection

An experienced observer (Dr. Rayadin) estimated age-sex class conservatively to avoid classifying immature individuals as adults. Females were classified as adults if they had a dependent offspring; otherwise, they were classified as immatures. If adult males had flanges that extended laterally beyond the border of the face they were considered flanged; if they did not, they were considered unflanged. Unflanged males were categorized as adults if they had roughly adult body dimensions and had lost the lighter juvenile facial pigmentation; otherwise they were classified as immatures. Body mass was obtained by weighing the individual in the cage, and then subtracting the known weight of the empty cage from the total weight.

Reanalysis of previously published orangutan body mass measurements

To determine differences between our body mass data and those published previously for Bornean orangutans,

TABLE 1. Weights (kg) for orangutans recorded during this study

ID	Weight	Habitat	Infant/Mother
Flanged adult males			
Je	58	FP	N/A
Ha	62	OP	N/A
Kl	68	OP	N/A
Ti	69	OP	N/A
Ka	74	OP	N/A
Da	74	OP	N/A
Kr	75	FP	N/A
Yo	76	OP	N/A
Jo	78	OP	N/A
Ss	78	OP	N/A
Sa	79	OP	N/A
Su	97	FP	N/A
Mean	74		
Unflanged adult males			
Be	28	OP	N/A
Ga	36	OP	N/A
El	38	OP	N/A
Ph	51	OP	N/A
Nu	58	FP	N/A
Mean	40.5		
Adult females			
Ri	25	FP	Rr
De	29	FP	Dr
Ka	35	OP	Ki
Re	35	FP	Rn
Nn	36	FP	Na
Bo	39	OP	Br
Ro	48	OP	Rs
Mean	35.29		
Female immatures			
Ki	6	FP	Ka
Rn	5	FP	Re
Dr	5	FP	De
Se	12	OP	N/A
Ru	21	FP	N/A
Male immatures			
Rr	6	FP	Ri
Na	7	FP	Nn
Br	9	OP	Bo
Rs	13	OP	Ro

TABLE 2. Weights (kg) for orangutans recorded by Lyon (1911), with immature or gutted individuals excluded following Markham and Groves (1990)

Catalog number	Weight
Adult males	
145301	90.72
145304	81.65
145305	79.38
153823	90.72
Mean	85.62
Adult females	
145300	32.66
145302	45.36
145306	37.20
153805	39.92
Mean	38.78

Catalog numbers are the originals provided by Lyon (1911) and are provided to permit identification of specimens.

we needed access to individual body mass measurements. Only means and ranges were presented in the most recent analysis performed by Markham and Groves (1990), so to obtain individual measurements we returned to the original data sources (Lyon, 1907, 1908, 1911). Upon reexamination we found small inconsistencies in Markham and Groves' (1990) reanalysis and presentation of these data. For example, they report excluding two of the five Bornean orangutan males presented in Lyon (1911) due to the fact that these males were not fully adult; however, in their final estimation of adult male body mass they report a sample size of $n = 4$, not $n = 3$. There are also some small discrepancies between the final means we calculated based on Lyon's (1911) data and those reported by Markham and Groves (1990). It is impossible to determine the source of these inconsistencies because Markham and Groves (1990) did not report all individual body mass measurements. We also chose to exclude the one measurement for a Bornean female included in Markham and Groves (1990) that was provided by Schultz (1941), since this measurement was taken on a captive individual. Thus for comparative purposes we reanalyzed Lyon's (1911) original data, following the guidelines of Markham and Groves (1990) and excluding all individuals that were not recorded as adult or were reported as being gutted before weighing. This left us with a sample size of $n = 4$ adult males and $n = 4$ adult females for body mass measurements of Bornean orangutans reported in previous studies.

RESULTS

Body mass for adult males ($n = 12$ flanged and $n = 5$ unflanged), adult females ($n = 7$), immature males ($n = 4$), and immature females ($n = 5$) from our study are presented in Table 1. When compared to the body masses for adult Bornean orangutans obtained by examining data presented in a previous study (Lyon, 1911) (Table 2), the average body mass of flanged adult males in our study is 13.6% lower (our study: $n = 12$, mean: 74 $\pm$ 9.78 kg, Lyon: $n = 4$, mean: 85.62 $\pm$ 5.96 kg; Mann–Whitney $U = 44$, $P < 0.05$) and the average body mass of adult females is 9% lower (our study: $n = 7$, mean: 35.29 $\pm$ 7.32 kg, Lyon: $n = 4$, mean: 38.78 $\pm$ 5.31 kg; Mann–Whitney $U = 19$, $P > 0.05$). The degree of sexual dimorphism is also slightly lower for our sample; Lyon's data indicate that that adult females were on average 45.3% the size of flanged adult males, but for our study this figure is 47.8%. Flanged adult males captured in oil palm (OP) for our study were smaller, on average, than those captured in forestry plantations (FP), with females exhibiting the opposite pattern, although samples sizes were too small to test statistically (Female OP: $n = 3$, mean = 40.67 $\pm$ 6.66 kg, Female FP: $n = 4$, mean = 31.25 $\pm$ 5.19 kg; Flanged male OP: $n = 7$, mean = 73.11 $\pm$ 5.67 kg; Flanged male FP: $n = 3$, mean = 76.67 $\pm$ 19.55 kg).

DISCUSSION

The body mass measurements for adult individuals reported here are on average lower for both flanged adult males and adult females than those from the only previously published data on wild Bornean orangutan body mass (Lyon, 1911). This difference was more pronounced for males than for females, with average flanged adult male body mass for this study significantly lower than that reported by Lyon. Interestingly, although average adult body mass reported in our study was lower, we reported a wider range of body mass measurements for both sexes than did Lyon.

We see three possible explanations (not mutually exclusive) for the differences between our results and those obtained from Lyon's (1911) data. First, differences between Lyon's data and this study may be an artifact of sampling. The sample size obtained from Lyon's data was relatively small (4 males and 4 females), and the individuals were all from northwestern or southwestern Borneo (Lyon, 1911). There is well-documented geographic variation in ecology, behavior, and morphology of orangutans across their range (Wich et al., 2009), which has resulted in the Bornean species (*Pongo pygmaeus*) being divided into three subspecies: the Northwest Bornean orangutan (*P.p. pygmaeus*), the Central Bornean orangutan (*P.p. wurmbii*), and the subspecies that is the focus of this study, the Northeast Bornean orangutan (*P.p. morio*). *P.p. morio* may have developed specialized morphological and behavioral strategies in response to pronounced resource scarcity and unpredictability in eastern Borneo (e.g., Taylor, 2006, 2009; Knott et al., 2009; Singleton et al., 2009; van Schaik et al., 2009). For example, *P.p. morio* exhibits smaller cranial capacity and larger, more robust jaws than Sumatran or other Bornean orangutan subspecies (Taylor, 2006, 2009), presumably as adaptations to diets that include a higher proportion of difficult-to-process fallback foods such as pith and inner bark. These differences may extend to a reduction of metabolically expensive large body size in *P.p. morio*.

A second possible explanation for the differences between our study and Lyon's data, specifically the large range in body sizes for adults reported in our study, is the difference in methods for determining maturity between the studies. Orangutans can exhibit delayed physical maturity, continuing to grow and develop well after sexual maturity is achieved (Fooden and Izor, 1983; Galdikas, 1985). This is especially true for adult males, who exhibit two different morphs—flanged and unflanged—and may live for years as unflanged males before transitioning into the flanged state (Utami et al., 2002; Utami Amoko et al., 2009). Lyon (1911) used the emergence of the third molar as a measure of maturity for both males and females, and the reliability of this feature in determining maturity was later confirmed by the examination of the skulls of the same specimens for the closure of the spheno-occipital suture, usually considered a definitive measure of maturity (Markham and Groves, 1990). Examining these features were not possible for our study animals, and we relied instead on a set of indicators that included the presence or absence of secondary sexual characteristics (such as laterally expanded cheek pads in the case of adult flanged males), other indirect indicators like body dimensions and facial pigmentation, and in the case of females, the presence of dependent offspring. We are confident in our classification of adult females, since all adult females in this study had a dependent offspring, which is usually a good indicator of physical maturity in wild animals, and in our classification of flanged adult males, who all clearly exhibited laterally expanded cheek pads. "Full maturity" is more difficult to determine for unflanged males and although we are confident in our assessments it is possible that males included in our unflanged adult male sample may not have been fully mature. In general, we acknowledge that the different measures used to gauge maturity for our study and Lyon (1911) may have led to some differences in the categorization of individuals and the possible inclusion of individuals who were not fully mature in our sample, contributing to the differences seen between the studies.

Finally, habitat disturbance and heterogeneity may explain the lower averages but wider range of adult male and female body mass measurements reported here. All orangutans included in this study were captured in forestry and oil palm plantations. Disturbed landscapes can reduce individual health and body condition due to reduced resource availability/quality, increased exposure to predators, or increase in contact and conflict with humans (Chapman and Peres, 2001; Irwin, 2008a,b). Such physical deterioration can be seen in measures of physiological condition (e.g., parasite load) and reduced body mass (Irwin et al., 2010). This may be evidenced in the orangutans in our study, with an interesting caveat: the fact that the range of body mass for flanged adult males and adult females in our study was so wide suggests that some individuals are doing well in these landscapes while some individuals are subject to energetic stress. This may reflect the heterogeneity of resource distribution in plantation habitats; some individuals may have had access to areas with relatively abundant resources (e.g., young acacia stands, or natural forest patches containing large fruiting trees) while others may have been utilizing less favorable microhabitats. Given the rapidly changing nature of the plantation landscapes and the limitations of our data set, we cannot correlate body mass with habitat condition, but anecdotal evidence supports this explanation. For example, one of the adult males with the lowest body mass (El, 38 kg) was captured in a small isolated natural forest patch (<10 ha) in an oil palm plantation. According to plantation management he had been living in this small patch for nearly six months. At the time of capture he was extremely emaciated, presumably as a result of lack of access to resources (Fig. 3a,b). This suggests that without proper land-use planning, including maintaining large natural forest patches and suitable connectivity between patches, plantations cannot provide suitable habitat for orangutans. Further study examining the behavior, ecology, and health of orangutans living in human-dominated landscapes is crucial to determining how to best manage these populations for long-term survival.

We acknowledge that this data set is limited and conclusions drawn from these data must be tentative. However, body size data from wild primates are crucial to allometric studies focused on understanding the relationship between body size and ecological and behavioral adaptations (e.g., Jungers, 1985), and we present these data so other researchers may use them. When the unfortunate opportunity presented by orangutan relocations arises, we encourage researchers to collect information on body mass as well as other physiological data (e.g., blood samples to assess white blood cell count, mineral and protein content, and the presence of infectious agents) that will allow us to monitor the health of orangutan populations (Kilbourn et al., 2003; Labes et al., 2010). Researchers could also begin employing alternative techniques that do not require the capture of animals to obtain information about body mass. Photogrammetry, or making measurements on photographs (Baker, 1960), has been used to estimate the body size and condition of mammals, including some primates (e.g., McFadden et al., 2006; Breuer et al., 2007, 2012; Berger, 2012; Kurita et al., 2012). The growing popularity of camera traps provides an opportunity for

Fig. 3. (**a**,**b**) Unflanged adult male El (38 kg) at the time of capture. Note his emaciation, which accounts for his exceptionally low body mass.

using such techniques to assess body condition in wild primates, although care must be taken to maximize the likelihood of obtaining standardized photographs. Ideally, if researchers begin regularly collecting such information for orangutans (and other primates), these data could be contributed to an open-access database that would allow comparisons of body mass/conditions across a range of geographic locations and habitat types, and could provide the ability to monitor population status over time. As orangutan habitat becomes increasingly fragmented and altered by humans, the need to make conservation decisions about orangutans living in human-dominated landscapes will become more frequent. Baseline data on body mass and physiological indicators of health from populations living in less disturbed settings and comparative data from animals living under various regimes of disturbance will be critical to our ability to make informed management decisions.

ACKNOWLEDGMENTS

The authors would like to thank Amir Ma'ruf, veterinarian from the Department of Forestry's Research Center for Natural Resources Conservation (BALITEK KSDA); Rido and Rifai from the Government Agency of Natural Resources Conservation (BKSDA); Tandya Tjahyana, head of BKSDA; Supriyono, Environmental Manager of PT Surya Hutani Jaya and PT Sumalindo Hutani Jaya; Donny Priandono, Sustainability Manager from Teladan Prima Group; Hendra Masrun, Nur Komari, Sugihono Hanggito, Ari Meididit and Junaedi Samsudin of the Ecology and Conservation Center for Tropical Studies (ECOSITROP) for their work on GIS and remote sensing; Erik Meijaard and Marc Ancrenaz for their assistance and helpful comments. All research was conducted in compliance with the institutional guidelines and legal requirements for the ethical treatment of animals in Indonesia. Dr. Yaya Rayadin has received consultant fees from Ecositrop as coordinator of research projects for orangutan conservation. The funding for these fees was provided by PT Surya Hutani Jaya, PT Sumalindo Hutani Jaya, PT Telen, PT Sawit Prima Nusantara, PT Telen Prima Sawit, and PT Gemilang Sejahtera Abadi.

LITERATURE CITED

Ancrenaz M, Oram F, Ambu L, Lackman I, Ahmad E, Elahan H, Kler H, Abram NK, Meijaard E. 2014. Of Pongo, palms and perceptions: a multidisciplinary assessment of Bornean orang-utans (Pongo pygmaeus) in an oil palm context. Oryx FirstView 1–8, doi: 10.1017/S0030605313001270.

Baker WH. 1960. Elements of photogrammetry. New York: Ronald Press.

Bastian ML, Zweifel N, Vogel ER, Wich SA, van Schaik CP. 2010. Diet traditions in wild orangutans. Am J Phys Anthropol 143:175–187.

Bell RHV. 1971. A grazing ecosystem in the Serengeti. Sci Am 225:86–93.

Berger J. 2012. Estimation of body size traits by photogrammetry in large mammals to inform conservation. Conserv Biol 26:769–777.

Breuer T, Robbins MM, Boesch C. 2007. Using photogrammetry and color scoring to assess sexual dimorphism in wild western gorillas (Gorilla gorilla). Am J Phys Anthropol 134:369–382.

Breuer T, Robbins AM, Boesch C, Robbins MM. 2012. Phenotypic correlates of male reproductive success in western gorillas. J Hum Evol 62:466–472.

Calder WA. 1984. Size, function, and life history. Cambridge: Harvard University Press.

Campbell-Smith G, Simanjorang HV, Leader-Williams N, Linkie M. 2010. Local attitudes and perceptions toward crop-raiding by orangutans (Pongo abelii) and other nonhuman primates in northern Sumatra, Indonesia. Am J Primatol 72:866–876.

Campbell-Smith G, Campbell-Smith M, Singleton I, Linkie M. 2011a. Apes in space: Saving an imperilled orangutan population in Sumatra. PLoSOne 6:e17210.

Campbell-Smith G, Campbell-Smith M, Singleton I, Linkie M. 2011b. Raiders of the lost bark: Orangutan foraging strategies in a degraded landscape. PloSOne 6:e20962.

Chapman CA, Peres CA. 2001. Primate conservation in the new millenium: the role of scientists. Evol Anthropol 10:16–33.

Clutton-Brock TH, Harvey PH. 1977. Sexual dimorphism, socioeconomic sex ratio and body weight in primates. Nature 269: 797–800.

Curran LM, Trigg SN, McDonald AK, Astiani D, Hardiono YM, Siregar P, Caniago I, Kasischke E. 2004. Lowland forest loss in protected areas of Indonesian Borneo. Science 303:1000–1003.

Damuth J, MacFadden BJ. 1990. Body size in mammalian paleobiology: estimation and biological implications. Cambridge: Cambridge University Press.

Dutton CJ, Junge RE, Louis EE. 2003. Biomedical evaluation of free-ranging ring-tailed lemurs (Lemur catta) in Tsimanampetsotsa Strict Nature Reserve, Madagascar. J Zoo Wildlife Med 34:16–24.

Dutton CJ, Junge RE, Louis EE. 2008. Biomedical evaluation of free-ranging red ruffed lemurs (Varecia rubra) within the Masoala National Park, Madagascar. J Zoo Wildlife Med 39: 76–85.

Eckhardt RB. 1975. The relative body weights of Bornean and Sumatran orangutans. Am J Phys Anthropol 42:349–350.

Fooden J, Izor RJ. 1983. Growth curves, dental emergence norms, and supplementary morphological observations in known-age captive orangutans. Am J Primatol 5:285–301.

Galdikas BMF. 1985. Adult male sociality and reproductive tactics among orangutans at Tanjung Puting. Folia Primatol 45: 9–24.

IUCN 2014. IUCN Red List of Threatened Species. Version 2014.2.

Irwin MT. 2008a. Feeding ecology of diademed sifakas (*Propithecus diadema*) in forest fragments and continuous forest. Int J Primatol 29:95–115.

Irwin MT. 2008b. Diademed sifaka (Propithecus diadema) ranging and habitat use in continuous and fragmented forest: higher density but lower viability in fragments? Biotropica 40:231–240.

Irwin MT, Junge RE, Raharison JL, Samonds KE. 2010. Variation in physiological health of diademed sifakas across intact and fragmented forest at Tsinjoarivo, eastern Madagascar. Am J Primatol 72:1013–1025.

Junge RE, Louis EE. 2005a. Preliminary biomedical evaluation of wild ruffed lemurs (*Varecia variegata* and *V. rubra*). Am J Primatol 66:85–94.

Junge RE, Louis EE. 2005b. Biomedical evaluation of two sympatric lemur species (*Propithecus verreauxi deckeni* and *Eulemur fulvus rufus*) in Tsiombokibo Classified Forest, Madagascar. J Zoo Wildlife Med 36:581–589.

Junge RE, Louis EE. 2007. Biomedical evaluation of black lemurs (*Eulemur macaco macaco*) in Lokobe Reserve, Madagascar. J Zoo Wildlife Med 38:67–76.

Junge RE, Dutton CJ, Knightly F, Williams CV, Rasambainarivo FT, Louis EE. 2008. Comparison of biomedical evaluation for white-fronted brown lemurs (Eulemur fulvus albifrons) from four sites in Madagascar. J Zoo Wildlife Med 39:567–575.

Junge RE, Barrett MA, Yoder AD. 2011. Effects of anthropogenic disturbance on Indri (*Indri indri*) health in Madagascar. Am J Primatol 73:632–642.

Jungers WL. 1985. Body size and scaling of limb proportions in primates.In: Jungers WL, editor. Size and scaling in primate biology. New York: Plenum. p 345–381.

Kilbourn AM, Karesh WB, Wolfe ND, Bosi EJ, Cook RA, Andau M. 2003. Health evaluation of free-ranging and semi-captive orangutans (Pongo pygmaeus pygmaeus) in Sabah, Malaysia. J Wildlife Dis 39:73–83.

Kleiber M. 1961. Fire of life: an introduction to animal energetics. New York: Kreiger.

Knott CD. 1998. Changes in orangutan caloric intake, energy balance, and ketones in response to fluctuating fruit availability. Int J Primatol 19:1061–1079.

Knott CD. 2005. Energetic responses to food availability in the great apes: implications for hominid evolution.In: Brockman DK, van Schaik CP, editors. Seasonality in primates: studies of living and extinct human and nonhuman primates. Cambridge: Cambridge University Press. pp 351–378.

Knott CD, Emery Thompson M, Wich SA. 2009. The ecology of female reproduction in wild orangutans.In: Wich SA, Utami Atmoko SS, Mitra Setia T, van Schaik CP, editors. Orangutans: geographic variation in behavioral ecology and conservation. Oxford: Oxford University Press. pp 171–188.

Kurita H, Suzumura T, Kanchi F, Hamada Y. 2012. A photogrammetric method to evaluate nutritional status without capture in habituated free-ranging Japanese macaques (*Macaca fuscata*): a pilot study. Primates 53:7–11.

Labes EM, Hegglin D, Grimm F, Nurcahyo W, Harrison ME, Bastian ML, Deplazes P. 2010. Intestinal parasites of endangered orangutans (Pongo pygmaeus) in Central and East Kalimantan, Borneo, Indonesia. Parasitology 137:123–135.

Laurance WF, Vasconcelos HL, Lovejoy TE. 2000. Forest loss and fragmentation in the Amazon: implications for wildlife conservation. Oryx 34:39–45.

Lindstedt SL, Boyce MS. 1985. Seasonality, fasting endurance, and body size in mammals. Am Natural 125:873–878.

Lyon MW. 1907. Mammals collected in western Borneo by Dr W.L. Abbott. Proc US Nat Mus 33:547–571.

Lyon MW. 1908. Mammals collected in eastern Sumatra by Dr W.L. Abbott during 1903, 1906 and 1907, with descriptions of new species and subspecies. Proc US Nat Mus 34:619–679.

Lyon MW. 1911. Mammals collected by Dr W.L. Abbott on Borneo and some of the small adjacent islands. Proc US Nat Mus 40:53–146.

MacKinnon JR. 1974. The behaviour and ecology of wild orangutans (Pongo pygmaeus). Anim Behav 22:3–74.

Markham R, Groves CP. 1990. Brief communication: weights of wild orang utans. Am J Phys Anthropol 8:1–3.

Marshall AJ, Boyko CM, Feilen KL, Boyko RH, Leighton M. 2009a. Defining fallback foods and assessing their importance in primate ecology and evolution. Am J Phys Anthropol 140: 603–614.

Marshall AJ, Engström LM, Pamungkas B, Palapa J, Meijaard E, Stanley SA. 2006. The blowgun is mightier than the chainsaw in determining population density of Bornean orangutans (*Pongo pygmaeus morio*) in the forests of East Kalimantan. Biol Conserv 129:566–578.

Marshall AJ, Lacy R, Ancrenaz M, Byers O, Husson SJ, Leighton M, Meijaard E, Rosen N, Singleton I, Stephens S, Traylor-Holzer K, Utami Atmoko SS, van Schaik CP, Wich SA. 2009b. Orangutan population biology, life history, and conservation. Perspectives from population viability analysis models. In: Wich S, Utami Atmoko SS, Mitra Setia T, van Schaik CP, editors. Orangutans: geographic variation in behavioral ecology and conservation. Oxford: Oxford University Press. pp 311–326.

Marshall AJ, Nardiyono, Engstrom LM, Pamungkas B, Palapa J, Meijaard E, Stanley SA. 2006. The blowgun is mightier than the chainsaw in determining population density of Bornean orangutans (*Pongo pygmaeus morio*) in the forests of East Kalimantan. Biol Conserv 129:566–578.

McFadden K, Lacher T, Worthy G. 2006. Photogrammetric estimates of size and mass in Hawaiianmonk seals (*Monachus schauinslandi*). Aquat Mammals 32:31–40.

McHenry HM. 1992. How big were early hominids? Evol Anthropol 1:15–20.

McHenry HM. 1994. Behavioural implications of early hominid body size. J Hum Evol 27:77–87.

Meijaard E, Albar G, Rayadin Y, Ancrenaz M, Spehar SN. 2010a. Unexpected ecological resilience in Bornean Orangutans and implications for pulp and paper plantation management. PloS ONE 5:e12813.

Meijaard E, Buchori D, Hadiprakarsa Y, Utami-Atmoko SS, Nurcahyo A, Tjiu A, Mengersen K. 2011. Quantifying killing of orangutans and human-orangutan conflict in Kalimantan, Indonesia. PloS ONE 6:e27491.

Meijaard E, Wich SA, Ancrenaz M, Marshall AJ. 2012. Not by science alone: why orangutan conservationists must think outside the box. Ann NY Acad Sci 1249:29–44.

Mitani JC. 1989. Orangutan activity budgets: monthly variations and the effects of body size, parturition, and sociality. Am J Primatol 18:87–100.

Permenhut 48. 2008. Pedoman penangulangan konflik antara Manusia dan Satwa Liar (Indonesian Law for Standard Operating Procedure for resolving conflicts between humans and wildlife). Jakarta: Government of the Republic of Indonesia.

Rijksen HD. 1978. A field study on Sumatran orang utans (Pongo pygmaeus abelii, Lesson 1827): ecology, behaviour and conservation. Netherlands: H. Veenman.

Rodman PS. 1977. Feeding behavior of orangutans in the Kutai Reserve, East Kalimantan.In: Clutton-Brock TH, editor. Primate ecology. London: Academic Press. pp 383–413.

Ruff CB, Trinkaus E, Holliday TW. 1997. Body mass and encephalisation in Pleistocene Homo. Nature 387:173–174.

Schultz, AH 1941. Growth and development of the orang-utan. Carnegie Inst. Wash. Publ., Contrib. Embryo]. 29:57–110.

Singleton I, Knott CD, Morrogh-Bernard HC, Wich SA, van Schaik CP. 2009. Ranging behavior of orangutan females and social organization.In: Wich SA, Utami Atmoko SS, Mitra Setia T, van Schaik CP, editors. Orangutans: geographic variation in behavioral ecology and conservation. Oxford: Oxford University Press. p 205–214.

Smith RJ, Pilbeam DR. 1980. Evolution of the orang-utan. Nature 284:447–448.

Sodhi NS, Koh LP, Brook BW, Ng PKL. 2004. Southeast Asian biodiversity: an impending disaster. Trends Ecol Evol 19:654–660.

Spocter MA, Manger PR. 2007. The use of cranial variables for the estimation of body mass in fossil hominins. Am J Phys Anthropol 134:92–105.

Taylor AB. 2006. Feeding behavior, diet, and the functional consequences of jaw form in orangutans, with implications for the evolution of *Pongo*. J Hum Evol 50:377–393.

Taylor AB. 2009. The functional significance of variation in jaw form in orangutans.In: Wich SA, Utami Atmoko SS, Mitra Setia T, van Schaik CP, editors. Orangutans: geographic variation in behavioral ecology and conservation. New York: Oxford University Press. p 15–32.

Utami Atmoko SU, Setia TM, Goossens B, James SS, Knott CD, Morrogh-Bernard HC, van Noordwijk MA. 2009. Orangutan mating behavior and strategies.In: Wich SA, Utami Atmoko SS, Mitra Setia T, van Schaik CP, editors. Orangutans: geographic variation in behavioral ecology and conservation. New York: Oxford University Press. p 235–244.

Utami SS, Goossens B, Bruford MW, de Ruiter JR, van Hooff JA. 2002. Male bimaturism and reproductive success in Sumatran orang-utans. Behav Ecol 13:643–652.

van Noordwijk MA, van Schaik CP. 2005. Development of ecological competence in Sumatran orangutans. Am J Phys Anthropol 127:79–94.

van Schaik CP, Marshall AJ, Wich SA. 2009. Geographic variation in orangutan behavior and biology.In: Wich SA, Utami Atmoko SS, Mitra Setia T, van Schaik CP, editors. Orangutans: geographic variation in behavioral ecology and conservation. New York: Oxford University Press. p 351–362.

Vogel ER, Haag L, Mitra-Setia T, van Schaik CP, Dominy NJ. 2009. Foraging and ranging behavior during a fallback episode: *hylobates albibarbis* and *Pongo pygmaeus wurmbii* compared. Am J Phys Anthropol 140:716–726.

Vogel ER, van Woerden JT, Lucas PW, Utami Atmoko SS, van Schaik CP, Dominy NJ. 2008. Functional ecology and evolution of hominoid molar enamel thickness: pan troglodytes schweinfurthii and Pongo pygmaeus wurmbii. J Hum Evol 55:60–74.

Wheatley BP. 1982. Energetics of foraging in *Macaca fascicularis* and *Pongo pygmaeus* and a selective advantage of large body size in the orang-utan. Primates 23:348–363.

Wheatley BP. 1987. The evolution of large body size in orangutans: a model for hominoid divergence. Am J Primatol 13: 313–324.

Wich SA, Gaveau D, Abram N, Ancrenaz M, Baccini A. 2012. Understanding the impacts of land-use policies on a threatened species: is there a future for the Bornean Orang-utan? PLoS ONE 7:e49142.

Wich SA, Meijaard E, Marshall AJ, Husson SJ, Ancrenaz M, Lacy RC, van Schaik CP, Sugardjito J, Simorangkir T, Traylor-Nolzer K., Galdikas BMF, Doughty M, Supriatna J, Dennis R, Gumal M, Knott CD, Singleton I. 2008. Distribution and conservation status of the orang-utan (*Pongo* spp.) on Borneo and Sumatra: how many remain? Oryx 42:329–339

Wich SA, Utami Atmoko SS, Mitra Setia T, van Schaik CP. 2009. Orangutans: geographic variation in behavioral ecology and conservation. Oxford: Oxford University Press.

Wich SA, Utami-Atmoko SS, Setia TM, Rijksen HD, Schürmann C, Van Hooff, JARAM, van Schaik CP. 2004. Life history of wild Sumatran orangutans (Pongo abelii). J Hum Evol 47:385–398.