

Do Orangutans Have Digestion Problems After Eating Oil Palm Fruit? *A Review*

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Abstract

This review discusses the assumptions of orangutans using oil palm by reviewing the daily activities and dietary composition of feeding behavior in wild and ex-rehabilitant orangutans. The percentage pattern of daily activity shows the same trend, spending more time on feeding than other activities. Similarly, the diet composition of wild or ex-rehabilitant orangutans in Sumatera and Borneo show the choice of fruit as their main diet, as a frugivore animals. However, when the fruit season decreases, both wild and ex-rehabilitant orangutans' choice to use bark or termites to meet their nutritional needs. There are three assumptions in this paper, First, forest fruit scarcity will drive orangutans to utilize other food resources. Second, based on ape dietary studies on oil palm fruit, chimpanzees, orangutans and gorillas preferred bark and young leaves rather than the fruit. Third, health problems arise after consuming oil palm fruit. This is an early sign that nutrients do not drive orangutan to consume oil palm fruit.

Keywords: oil palm, orangutans, digestion, nutrition

INTRODUCTION

The amount of forest cover in Indonesia is declining drastically. The World Research Institute (WRI) reported that from 1990 to 2000, Indonesia lost 1.78 million hectares of forest cover, and five years later 0.71 million hectares of forest was converted to the other forms of land use (Hansen, 2009). This current change to forest cover has increased due to the number of natural resource concession permits granted by the Indonesia government. For example, the total land for oil palm plantations in 2008 was 7,363,847 hectares and in 2019 the total area increased to 14,456,611 hectares (Direktorat Jenderal Perkebunan, 2020).

Over the last 10 years, almost 80 percent of this land use change has occurred in the habitats of orangutans, or overlapped with forest that consists of the High Conservation Values (HCVs). Based on the orangutan distribution published by Forum Orangutan Indonesia (2013), 70 percent of orangutans are distributed outside of protected forests; this is a result of the forest being converted for other land uses such as forest concession and agriculture, and economic development. The same condition was also reported by Meijaard and Wich (2007), who found that overall, loss of orangutan habitats in Borneo was estimated at 3,122 km² per year between 1990 and 2004. This overlapping orangutan distribution with concession areas is leading to a large conflict between orangutan and humans (Yuwono et al., 2007).

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Currently, conflict between orangutans and oil palm companies has impacted the diet of the orangutans. Orangutans are confined to a very small habitat with limited food resources. It has been observed that orangutans will eat both the young stems of oil palm trees and their fruits; but in many cases orangutans prefer the stem instead of the fruit (Yuwono et al., 2007; Campbell-Smith et al., 2011 and Prasetyo, personal observation). There is limited data on why orangutans prefer the young stems of palm oil trees over palm oil fruits, but this preference may be due to the high lipid concentration in the fruits that adversely affects their digestive function. This research paper will discuss the orangutan diet among wild populations in their natural habitats and of orangutans living in proximity to oil palm plantations. In addition, there will be a review of research investigating several possibilities to answer the question why orangutans do not eat the oil palm fruits as much as the stems. We will discuss digestive physiology and the nutritional properties of palm fruits in relationship to the nutritional properties of their diets in the wild. We will also provide case studies from other primate species to serve as a comparison.

ORANGUTAN'S DIET COMPOSITION

Orangutans are frugivorous primates, spending more time feeding on fruits than leaves, bark, or insects. Based on the comparison from nine orangutan distribution sites, orangutans eat about 60% of fruits in their diet (Morrogh-Bernard et al., 2009). Russon et al. (2009) compared the orangutan diet of 15 orangutan research stations representing three orangutan sub-species and found that 1486 plant species are used by orangutans. Based on their report, the mean percentage of eaten fruits is higher for the Sumatran orangutan species compared to the Bornean orangutan, 75 of 149 plant species were consumed by Sumatran orangutans and 69 of 151 plant species identified eat by Bornean orangutans (Russon et al., 2009). The differences among orangutans' diet is affected by the resources available to them. For instance, Sumatra forests generally have a high quality and quantity of fruits relative to Borneo forests (Marshall et al., 2009; Wich et al., 2011).

To adapt to the lower levels of fruit availability, Bornean orangutans appear to be more flexible and use other food resources such as flowers, leaves, pith, and cambium than Sumatran orangutans (mean Bornean orangutans= 0.07, 0.33, 0.06, 0.16; and mean Sumatran orangutans= 0.03, 0.1, 0.05 and 0.04) (Russon et al., 2009). A comparison of diet composition between age-sex classes was also analyzed by Morrogh-Bernard et al. (2009), who found a trend that female orangutans feed more often than males; in contrast if the comparison is conducted between orangutan species, Sumatran orangutans spend a greater percentage of time feeding than Bornean orangutans. On the other hand, there is a trend for non-sexually active female of ex-rehabilitant orangutans in Kehje Sewen to spend more time feeding. The immature ex-rehabilitant orangutans show feeding time accounted for the largest part of the released orangutan's activity budget during the first-year post-release. They clearly spent more time feeding fruit than leaves, bark or invertebrates and others (soil, water, grass etc.) in Bukit Tiga Puluh, Tanjung Puting and Sungai Wain (Riedler et al. 2010; Russon et al. 2009; Basalamah et al. 2017).

The differences between forest production and food availability will have an effect on feeding activity. When orangutans are distributed in masting forests or when the food supply is more irregular, orangutans will spend less than 50% feeding and spend more time resting (Morrogh-Bernard et al., 2009). This pattern was also reported by Knott (1998) for Bornean orangutans; when fruits were limited, orangutans ate more bark (37%) than fruits (21%). This behavior changed when fruit availability was higher. Variation in feeding behavior in relationship to fruit abundance was also studied in logged forest (Morrogh-Bernard et al., 2009; Hardus et al., 2012), pulp and paper concession (Meijaard et al., 2010), and crop-raiding (Campbell-Smith, 2010). As frugivores, orangutans preferred fruits as their priority food, even when living in logged forest. But the use of other food resources (e.g. leaves, bark, and insects) increased in logged forests compared to the unlogged forests (Hardus et al., 2012).

Dietary information for orangutans living inside oil palm plantations is not readily available; several unpublished records suggest that sometimes orangutans include oil palm fruit in their diets when the food availability in the forest is poor. Campbell-Smith et al. (2011) discussed the Sumatran orangutan diet composition in the cultivated site (including oil palm plantation) and found that 16 orangutans ate nine cultivated species, and they also frequently ate domesticated fruits (i.e., *Artocarpus heterophyllus, Durio sp, Archidendron pauciflorum, Parkia speciosa*) in addition to the oil palm fruit. When oil palm trees are used as a food resource, orangutans preferred young leaves over fruits and bark for cambium extraction.

OIL PALM NUTRITION FACT

African palm oil (*Elaeis guineensis*) was found in the 1400s in West Africa and commonly began being planted in the 1800s (Opsomer, 1956 cited in Corley and Tinker, 2003). Palm oil plantations in Indonesia were planted in Sumatra in 1911 using Deli Palms. Oil palm plantation development grew in 1925, with 31,600 hectares of plantation established in Sumatra. This number is higher than development in Malaysia, which was only 3,350 hectares during that time (Corley and Tinker, 2003).

Palm oil fruit is divided into two major parts: mesocarp and kernel. The mesocarp, often referred to as pulp, is the majority of the palm oil fruit, making up about 71-76% of the whole fruit. The kernel or seed is only about 20% of the fruit structure (www.fao.org). Almost 100% of the mesocarp contains lipids and the palm oil kernel is made of 47–52% of oil (Hartley, 1988 cited in Corley and Tinker, 2003). The U.S. Department of Agriculture reported in 2003 that the nutrient composition of oil palm per 100 gram is made 49.3 grams of saturated fatty acid, 37 grams of monounsaturated fatty acid, 9.3 grams of polyunsaturated fatty acid, 0.01 mg of Iron, 0.3 mg of Choline, 15.94 mg of Vitamin E, and 8 μ g of Vitamin K (USDA, 2013).

ORANGUTAN'S DIGESTIVE SYSTEM AND COPING WITH LIPIDS

Great apes are a hindgut fermenter (Lambert and Fellner, 2011) or caeco-colic fermenters (Lambert, 1998). A caeco-colic fermentation system is divided into two chambers, caecum and colon; and is more efficient for mammals that rely on digestible foods components (Lambert, 1998). Gastrointestinal anatomy and the digestive system are the result of adaptations to chemical, physical, and nutritional properties of diet. With these adaptations, primates show the differential of an adaptations in their gut, included the stomach, caecum, and colon (Lambert, 1998). Milton (1987) measured the proportion of



relative gut volume in orangutans and found that they have smaller stomachs (17%) compared to gorillas and chimpanzees (25% and 20%). She also found as a great ape with caeco-colic fermentation system, orangutans have a smaller caecum and bigger colon than other great apes.

Lambert (1998) described that food digestion has four major steps: First step is ingestion, in which food is first procured and taken into the body by mechanical and enzymatic processes. Mechanical processes are identified based on teeth morphology. For example, the differences between enamel thicknesses of great apes are indicative of differentiation of food properties (Constantino et al., 2012; Vogel et al., 2007). An enzymatic process is facilitated by amylase, this enzyme is present in the saliva where help the hydrolysis process from starch into sugar. In primates, amylase enzyme was studied in Bonnet Macaque's cheek pouches, is a universal enzyme that facilitates starch digestion during the ingestion stage (Rahaman et al., 1975). The second step is digestion, a process in which food is broken down by both chemical and mechanical processes. Chemical processes involve amylase and other complex carbohydrate enzymes secreted by the liver and pancreas, whereas mechanical activity is known as peristaltic movement. In digestion process, protein is break down by chemical process of the liver and pancreas. There are three enzymes that are well known released by liver and pancreas to play an important role in protein digestion i.e., pepsin, trypsin, and chymotrypsin (Lambert, 1998). Furthermore, lipid digestion starts in the stomach and large intestine and is completed in the small intestine. Digestion and absorption of lipids occurs by a complex process that involves pancreas secretions, lipid emulsification, hydrolysis of fatty acid esters, and the absorption of the hydrolyzed products in the enterocyte (Castro, 1984 as cited in del Rio and Restrepo, 1993; Iqbal and Hussain, 2009). The third step of food digestion is absorption, the process in which digested food is passed to the cardiovascular and lymphatic systems for distribution to the cells. And the last process or fourth step is defecation, the process in which indigestible products are eliminated from the body.

The Kyoto Encyclopedia of Genes and Genomes has characterized the lipid digestive system pathway for orangutans (Fig 1, www.genome.jp/kegg). More than 95% of dietary fat is long-chain triacylglycerols, and the rest is phospholipids (4.5%) and sterols. The pancreas produces lipase to hydrolize fatty acids and monoacylglycerols from triacylglycerols. These products are mixed with the support of phospholipids and bile acids to form micelles. The absorption of emulsificated fat conduct in the intestinal wall, along with process of the hydrolisis of fat in the duodenum (Iqbal and Hussain, 2009).

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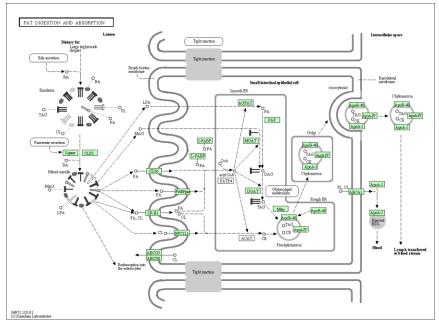


Figure 1. The lipids digestion pathway in Sumatran orangutan (www.genome.jp/kegg).

OIL PALM FRUIT IN THE ORANGUTANS (APES) DIET

Oil palm trees originally dispersed naturally in Africa and were not just planted in plantations (Corley and Tinker, 2003) but were known to overlap with the chimpanzees' habitat in places such as Bossou and Nimba Mountains in West Africa (Humle and Matsuzawa, 2004), Mahale Mountains in Tanzania (Zamma et al., 2011), Cantanhez National Park is located in Tombali Region, in Southern Guinea-Bissau (Sousa et al., 2011). Oil palm distribution also overlapped with gorilla habitat in the Lope Reserve, Gombe (Rogers et al., 1990). In contrast, oil palm trees are not reported as naturally dispersing in orangutan habitat.

Chimpanzees included the oil palm fruit in their diet, although the amount is very small and this occurs only when forest fruits are scarce (Humle and Matsuzawa, 2004; Sousa et al., 2011). Chimpanzees in Mahale also eat oil palm fruit. This is a new finding in the 1960s. Previously, chimpanzees did not include oil palm fruit into their diet, and the reason why they began consuming oil palm fruit is because they were inspired from local people who also used the oil palm tree (fruits) in their daily lives (Zamma et al., 2011). Interestingly, Gombe gorrilas at the Lope Reserve do not eat oil palm fruit even if its fruits are available in the forest. In contrast, Chimpanzees in the same place included the oil palm fruit in their diets (Rogers et al., 1990).

Orangutans very rarely eat oil palm fruit. Several surveys conducted in the oil palm plantations in Sumatra and Kalimantan found that orangutans eat very small amounts of oil palm fruit, but they eat more young stems of oil palm trees (personal observation). The same case was published by Campbell-Smith et al. (2011), who found that orangutans that are living in the crop-raiding habitat included oil palm trees as a food resource. Orangutans in that area consumed oil palm fruit, young leaves, and bark. However, when oil palm consumption is compared with other crop fruits (jackfruit, leguminous, durian) found in the same area, the amount of oil palm fruit consumption is small.

The reason why orangutans do not eat oil palm fruit has not been studied yet. Several assumptions will be discussed in this research paper to initiate earlier understanding of why orangutans do not consume oil palm fruit. First, forest fruit scarcity will drive orangutans to utilize other food resources. In the masting forest when fruits are limited, orangutans will consume another food resource. Knot (1998) found that when the fruit availability is low, orangutans consumed bark and flowers; this is contrasted by when the fruits are abundant, orangutans only consumed fruits. Plantations or forest reserve conservation areas usually have very low coverage. The Government of Indonesia does not regulate how much conservation area should be set aside as wildlife refuge. When the plantations are being built, many concessions only provide limited conservation area because of economic reasons.

Furthermore, the conservation area design does not consider animal needs. Orangutans living in this area have to deal with the small habitat as well as limited food resources and food scarcity. Meijaard et al. (2010) found orangutans that lived in the *Acacia sp* plantation consumed a lot of *Acacia sp*. bark when the fruit availability was low. In a different concession type, Campbell-Smith et al. (2011) recorded orangutans living in the crop-raiding area and oil palm plantation frequently consumed cultivated fruits rather than oil palm fruit. In contrast, Bossou chimpanzees more frequently consume oil palm when forest fruits are scare, but the proportion is not as great as the heart and petiole of oil palm trees (Humle and Matsuzawa, 2004). The same case was also reported by Yamakoshi (1998), where chimpanzees at Bossou consumed more oil palm pith than kernel.

The second assumption is that differential oil palm nutrients will drive food part choice. The nutritional analysis from oil palm mesocarp fruit shows that lipid is the major nutrient (75%), followed by water (25.2%), crude protein (2,08%), acid-digestible fiber (10.4%), and tannins (0.9%) (Rogers et al, 1990). The average composition of palm kernels is 47–52% oil, 6–8% moisture, 7.5–9% protein, 23–24% extractable non-nitrogen (mainly carbohydrates), 5% cellulose and 2% ash (Hartley, 1988 cited from Corley and Tinker, 2003). However, there are no reports about the nutrient components for oil palm pith, bark, and young leaves. As frugivores, orangutans should choose fruits based on the priority of food selection, and the nutrition in oil palm fruit is thought to be higher than other parts of the oil palm tree. Based on ape dietary studies on oil palm fruit, chimpanzees, orangutans and gorillas preferred bark and young leaves rather than the fruit. This is an early sign that nutrients do not drive orangutan and other ape species to consume oil palm fruit.

The third assumption is that health problems arise after consuming oil palm fruit. The effect has been studied in several mammals and primates, as well as humans (Sambanthamurthi et al., 2000, Ebrahimi et al., 2011, Ponnampalam et al., 2011, and van Jaarsveld et al., 2000). Early studies using rats as a model do not show significant results on how the oil palm affected cholesterol regulation and metabolism, since the rat is predominately a HDL animal model and it is difficult to induce hypercholesterolaemia or atherosclerosis. In contrast, studies conducted in hamsters and gerbils found that dietary cholesterol feeding induces significant changes in total plasma lipid and LDL-C (Sambanthamurthi et al., 2000). Diet experiments in goats with oil palm showed no significant effect on total fat content, monounsaturated fatty acid, and polyunsaturated fatty acid but, saturated fatty acid dominated with palmitic acid shown significantly in the goat's muscles (Ebrahimi et al., 2011). A dietary study on pediatric pigs eating natural palm oil did

not show significant results on weight gain, in contrast to significant results found when pigs were fed with enzymatic palm oil. In addition, the total cholesterol in the blood was lower when pigs were fed with natural palm oil instead of enzymatic palm oil (Ponnampalam et al., 2011).

The effect of oil palm was also studied in non-human primates. Van Jaarsveld et al. (2000) studied the plasma lipoprotein and plasma low-density lipoprotein (LDL) in vervet monkeys fed with oil palm and found that total plasma lipid in the high fat diet was lower than lard, but the composition of LDL-Cholesterol was higher. In contrast, when the fat diet was at a moderate level, the cholesterolaemic effect was not different between palm oil, lard, and sunflower. Another study was conducted in Cebus monkeys, replacing other fat properties (canola oil) with oil palm did not affect the plasma lipid concentrations and lipoprotein metabolism (LDL and HDL kinetics). Similar results were also apparent in another study using Cebus and rhesus monkeys given cholesterol-free diets. The palm oil diet also resulted in the lowest LDL/HDL cholesterol ratio, which was significantly better than the canola oil control diet (Hayes and Khosla, 1992, Sambanthamurthi et al., 2000). Studies on human diet supplemented with oil palm showed no significant results on total cholesterol and lipoprotein lipids, whereas a possible beneficial effect on apolipoprotein distribution was indicated (Sambanthamurthi et al., 2000).

CONCLUSION

As a frugivorous primate, orangutans prefer fruits in their diet. But when the fruits are scarce, orangutans frequently consume bark or leaves. Studies on orangutans' diet in the limited food resource environments (i.e., oil palm plantations) have been inconclusive. Due to the introduction of oil palm trees within the orangutan habitat, the oil palm stems, and leaves have become slightly incorporated into their diet; however, the fruits are avoided due to their physiological response. Ultimately, three assumptions reviewed in this research paper support oil palm stems as possible food source and avoidance of the oil palm fruit. It can be concluded that fruit availability in the forest does not drive orangutan consumption of the oil palm fruit but rather, the high lipid concentration in this fruit discourages them from feeding on it. Further, the impact on their health (e.g., digestive system) keeps orangutans from including oil palm fruit as a food preference. Studies on the fast chemical reactions of high lipid consumption in orangutans' stomachs may help find the answer to why orangutans do not consume much oil palm fruit.

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REFERENCES

- Basalamah, F., Utami-Atmoko, SS., Perwitasari-Farajallah, D., Qayim, I., Sihite, J., van Noordwijk M., Willems, E., van Schaik, CP. 2017. Monitoring orangutan reintroduction: Results of Activity Budgets, Diets, Verical Use and Associations during The First Year Post Release In Kehje Sewen Forest, East Kalimantan, Indonesia. Biodiversitas (19): 2, pages 689-700.
- Campbell-Smith, G., Simanjorang, H.V.P., 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. 2011. Raiders of the Lost Bark: Orangutan Foraging Strategies in a Degraded Landscape. PLoS ONE 6(6): e20962. doi:10.1371/journal.pone.0020962.
- Castro, G.A. 1984. Digestion and absorption. In: Johnson, L. R. (ed.). Gastrointestinal physiology. CV Mosby Co., St Louis Missouri, pages 105-128.
- Constantino, P.J., Lee, J.J.W., Gerbig, Y., Hartstone-Rose, A., Talebi, M., Lawn, B.R., & Lucas, P.W. 2012. The Role of Tooth Enamel Mechanical Properties in Primate Dietary Adaptation. Am J Phys Anthro 148:171-177.
- Corley, R.H.V., & Tinker, P.B. 2003. The Oil Palm. Fourth edition. Blackwell Science Ltd. 578 pages.
- Direktorat Jenderal Perkebunan. 2020. Statistik perkebunan unggulan nasional 2019-2021. Sekdirjen Perkebunan. Direktorat Jenderal Perkebunan, Kementerian Pertanian. 2020.
- Ebrahimi, M., Rajion, M.A., Goh, Y.M., Sazili, A.Q. 2011. Impact of different inclusion levels of oil palm (*Elaeis guineensis Jacq.*) fronds on fatty acid profiles of goat muscles. J Anim Phys and Anim Nutr 96: 962-969.
- Hansen, M.C., Stehman, S.V., Potapov, P.V., Arunarwati, B., Stolle, F. & Pittman, K. 2009. Quantifying changes in the rates of forest clearing in Indonesia from 1990 to 2005 using remotely sensed data sets. Environ Res Lett 4:034001. doi:10.1088/1748-9326/4/3/034001.
- Hardus, M.E., Lameira, A.R., Menken, S.B.J., & Wich, S.A. 2012. Effects of logging on orangutan behavior. Bio Cons 146:177-187.
- Hartley, C.W.S. 1988. The oil palm, 3rd edition, Longman, London.
- Hayes, K.C., & Khosla, P. 1992. Dietary fatty acid thresholds and cholesterolemia. The FASEB Journal 6:2600-2607.
- Humle, T., & Matsuzawa, T. 2004. Oil Palm Use by Adjacent Communities of Chimpanzees at Bossou and Nimba Mountains, West Africa. Intl J Primatol 3:551-581.
- Iqbal, J., & Hussain, M. 2009. Intestinal lipid absorption. Am J Physiol Endocrinol Metab 296(6): E1183–E1194.
- Knott, C.D. 1998. Changes in Orangutan Caloric Intake, Energy Balance, and Ketones in Response to Fluctuating Fruit Availability. Int J Primatol 19(6):1061-1079.

- Lambert, J.E. 1998. Primate Digestion: Interactions among Anatomy, Physiology, and Feeding Ecology. Evol Anthro 7(1):8-20.
- Lambert, J.E., & Fellner, V. 2011. In Vitro Fermentation of Dietary Carbohydrates Consumed by African Apes and Monkeys: Preliminary Results for Interpreting Microbial and Digestive Strategy. Int J Primatol 33:263-281. DOI 10.1007/s10764-011-9559-y.
- Marshall, A.J., Ancrenaz, M., Brearley, F.Q., Fredriksson, G.M., Ghaffar, N., Heydon, M., Husson, S.J., Leighton, M., McConkey, K.R., Morrogh-Bernard, H.C., Proctor, J., van Schaik, C.P., Yeager, C.P., & Wich, S.A. 2009. The effects of forest phenology and floristics on populations of Bornean and Sumatran orangutans. *In* Wich, S.A., Atmoko, S.S.U., Mitrasetia, T., & van Schaik, C.P. Geographic Variation in Behavioral Ecology and Conservation. Oxford University Press. Pages 97-118.
- del Rio, C.M., & Restrepo, C. 1993. Ecological and behavioral consequences of digestion in frugivorous animals. Vegetatio 107(108):205-216.
- Meijaard, E., & Wich, S.A. 2007. Putting orang-utan population trends into perspective. Current Biol 17(14) R540.
- Meijaard, E., Welsh, A., Ancrenaz, M., Wich, S.A., & Nijman, V. 2010. Declining Orangutan Encounter Rates from Wallace to the Present Suggest the Species Was Once More Abundant. PLoS ONE 5(8): e12042. doi:10.1371/journal.pone.0012042.
- Milton, K. 1987. Primate diets and gut morphology: Implications for hominid evolution. In Harris, M., & Ross, E.B. (eds), Food and Evolution: Toward a Theory of Human Food Habits, pages 93–115. Philadelphia: Temple University Press.
- Morrogh-Bernard, H.C., Husson, S.J., Knott, C.D., Wich, S.A., van Schaik, C.P., van Noordwijk, M.A., Lackman-Ancrenaz, I., Marshall, A.J., Kanamori, T., Kuze, N., & bin Sakong, R. 2009. Orangutan activity budgets and diet. *In* Wich, S.A., Atmoko, S.S.U., Mitrasetia, T., & van Schaik, C.P. Geographic Variation in Behavioral Ecology and Conservation. Oxford University Press. Pages 119-134.
- Nantha, H.S., & Tisdel, C. 2008. The orangutan–oil palm conflict: economic constraints and opportunities for conservation. Biodivers Conserv 18:487–502. DOI 10.1007/s10531-008-9512-3.
- Opsomer, J.K. 1956. Les premières descriptions de palmier à huile (*Elaeis guineensis Jacq.*). Bull Séances Acad R Soc Colon (Outre Mer), 2:253–272.
- Ponnampalam, E.N., Lewandowski, P., Nesaratnam, K., Dunshea, F.R. & Gill, H. 2011. Differential effects of natural palm oil, chemically and enzymatically-modified palm oil on weight gain, blood lipid metabolites and fat deposition in a pediatric pig model. Nutrition Journal 10:53.
- Rahaman, H., Srihari, K., & Krishnamoorthy, R.V. 1975. Polysaccharide Digestion in Cheek Pouches of the Bonnet Macaque. Primates 16(2): 175-180.
- Riedler B, Millesi E, Pratje PH. 2010. Adaptation to forest life during the reintroduction process of Immature Pongo abelii. International Jurnal Primatology (31): 647- 663.
- Rogers, M.E., Maisels, F., Williamson, E.A., Fernandez, M., & Tutin, C.E.G. 1990. Gorilla diet in the Lope Reserve, Gabon: A nutritional analysis. Oecologia 84:326-339.
- Russon, A.E., Wich, S.A., Ancrenaz, M., Kanamori, K., Knott, C.D., Kuze, N., Morrogh-Bernard, H.C., Pratje, P., Ramlee, H., Rodman, P., Sawang, A., Sidiyasa, K.,

Singleton, I., & van Schaik, C.C.P. 2009. Geographic variation in orangutan diets. *In* Wich, S.A., Atmoko, S.S.U., Mitrasetia, T., & van Schaik, C.P. Geographic Variation in Behavioral Ecology and Conservation. Oxford University Press. Pages 135-156.

- Sambanthamurthi, R., Sundram, K., & Tan, Y.A. 2000. Chemistry and biochemistry of palm oil. Progress in Lipid Research 39: 507-558.
- Sousa, J., Barata, A.V., Sousa, C., Casanova, C.C.N., & Vicente, L.S. 2011. Chimpanzee Oil-Palm Use in Southern Cantanhez National Park, Guinea-Bissau. Am J Primatol 73:485-497.
- USDA. 2013. National Nutrient Database for Standard Reference for oil palm. http://ndb.nal.usda.gov/
- van Jaarsveld, P.J., Smuts, C.M., Tichelaar, H.Y., Kruger, M., & Benad'e, A.J.S. 2000. Effect of palm oil on plasma lipoprotein concentrations and plasma low-density lipoprotein composition in non-human primates. Intl J Food Sci and Nutr 51:S21–S30.
- Vogel, E.R., van Woerden, J.T., Lucas, P.W., Atmoko, S.S.U., van Schaik, C.P., & Dominy, N.J. 2007. Functional ecology and evolution of hominoid molar enamel thickness: *Pan troglodytes schweinfurthii* and *Pongo pygmaeus wurmbii*. J Hum Evol 55: 60-74.
- Wich, S.A., Vogel, E.R., Larsen, M.D., Fredriksson, G., Leighton, M., Yeager, C.P., Brearley, F.Q., van Schaik, C.P., & Marshall, A.J. 2011. Forest Fruit Production Is Higher on Sumatra Than on Borneo. PLoS ONE 6(6): e21278. doi:10.1371/journal.pone.0021278.
- Yamakoshi, G. 1998. Dietary Responses to Fruit Scarcity of Wild Chimpanzees at Bossou, Guinea: Possible Implications for Ecological Importance of Tool Use. Am J Phys Anthropol 106:283-295.
- Yuwono, E.H., Susanto, P., Saleh, C., Andayani, N., Prasetyo, D., & Atmoko, S.S.U. 2007. Guidelines for the best management practices on avoidance, mitigation and management of human-orangutan conflict in and around oil palm plantations. WWF-Indonesia.
- Zamma, K., Nakashima, M., & Ramadhani, A. 2011. Mahale Chimpanzees Start to Eat Oil Palm. Pan Africa News 18:1.