

Meat-eating by a wild Bornean orang-utan (*Pongo pygmaeus*)

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Abstract We present the first evidence for consumption of meat by a wild Bornean orang-utan (*Pongo pygmaeus*). Meat-eating has been reported in Sumatran orang-utans, specifically the hunting and consumption of slow lorises (*Nycticebus coucang*), but loris-hunting behaviour has not been observed in the Bornean species and meat of any species is essentially absent from their diet, with only two anecdotal reports of vertebrate meat consumption prior to this current finding in over 40 years of study. In August 2012 an unhabituated adult flanged male orang-utan was observed eating an adult horse-tailed squirrel (*Sundasciurus hippurus*) carcass in the Sabangau peat-swamp forest, Central Kalimantan. We suspect this to be a case of scavenging, never reported previously in a Bornean orang-utan.

Keywords *Pongo pygmaeus* · Orang-utan · Borneo · Meat-eating · Scavenging

Introduction

Orang-utans (*Pongo* spp.) are predominantly frugivorous, but their diet also regularly includes a variety of other foods including leaves, flowers, bark and invertebrates (Russon et al. 2009). There are, however, a few instances in which orang-utans have been observed eating vertebrate meat. The cases published to date are from the research sites of Ketambe and Suaq Balimbing in Northern Sumatra. At Ketambe, two adult female orang-utans (*Pongo abelii*—one formerly rehabilitated and one wild) were observed to hunt slow lorises (*Nycticebus coucang*) on at least nine occasions, through a clear process of catching, killing and eating the prey (Utami and van Hooft 1997; Hardus et al. 2012). At Suaq Balimbing, one wild flanged male and two wild adult females were similarly observed to catch and eat slow lorises on one occasion each (van Schaik et al. 2009). In another account, a wild Sumatran adolescent female was reported to have eaten a gibbon (*Hylobates lar*) carcass, which appeared to have been scavenged (Sugardjito and Nurhuda 1981); this incident is now disputed as an episode of scavenging and thought to be another case of orang-utan predation of a slow loris (Rijksen and Meijaard 1999; Hardus et al. 2012). On Borneo, there are only two known accounts of orang-utans (*Pongo pygmaeus*) eating vertebrate meat. In Gunung Palung National Park (West Kalimantan) a wild juvenile female was seen catching and eating a rat (Knott 1999a), and in Tanjung Puting National Park, volunteers reported seeing a male orang-utan eat two baby squirrels from a squirrel nest (Dale 1986).

In this report, we document an event of meat-eating by a wild Bornean flanged male orang-utan (*Pongo p. wurmbii*). This individual was observed eating a squirrel carcass, which he appeared to have scavenged. We suggest that this

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is the first documented case of scavenging by a Bornean orang-utan, as well as the first fully documented report of an orang-utan eating squirrel meat.

Methods

The incident of meat-eating was observed during the dry season on 6th August 2012, during data collection on male ranging behaviour in the Sabangau peat-swamp forest, Central Kalimantan, Indonesia. This is the first instance of this behaviour in over 16,000 h of observational follow data, since the research project began in 2003.

This research was carried out as part of the OUTROP-CIMTROP multi-disciplinary research project in the Natural Laboratory of Peat Swamp Forest (2°19.002'S, 113°54.483'E). This is an area of selectively logged mixed peat-swamp forest within the greater Sabangau ecosystem (Fig. 1). This 5300 km² of continuous forest is home to the world's largest remaining orang-utan population, estimated to number 6900 individuals (Morrogh-Bernard et al. 2003; Wich et al. 2008). These orang-utans are the south-west Borneo subspecies (*Pongo p. wurmbii*), and no ex-captive or rehabilitant orang-utans have ever been released in the area.

The data presented here are direct observations by the first author.

Results

The subject of this report is a wild, unhabituated flanged male orang-utan, never previously followed by the observation team (Fig. 2a). He was found by the first author and his assistant at 1025 h local time on 6th August 2012, 3.85 km from the forest edge and 5.3 km from the Sabangau River (2°20.572'S, 113°53.186'E). He displayed no unusual behaviour while being followed by the observers, and proceeded to travel 160 m through the forest in a westerly direction during the first hour of the follow (Fig. 3). He travelled in the trees and did not descend to the forest floor during this time.

At 1131 h he stopped in a tree at a height of 10 m and began to eat an item in his hand. Observations were initially obstructed as the orang-utan continually turned his back on the observers as they attempted to get a clearer view from different angles. Crunching noises were heard, and the item being eaten was later identified as a squirrel carcass of size and colour consistent with an adult horse-tailed squirrel (*Sundasciurus hippurus*). The orang-utan's acquisition of the squirrel was not observed; there was no sign of a chase, no squeals had been heard leading up to this feeding bout, and there was no fresh blood from the

carcass; we reason, therefore, that the squirrel was probably already dead and that the orang-utan found it in the trees.

At the point when clear observations of the event were possible, the head was already missing from the squirrel carcass (Fig. 2b, c). The orang-utan, although occasionally using both hands, primarily held the carcass in his left hand, whilst pulling at the carcass with his teeth (Fig. 2d, e). At 1153 h the entrails of the squirrel were dropped (Fig. 2f), but every other part of the carcass was chewed and swallowed, including bones, skin, fur and tail. The total time spent feeding on the carcass was 41 min. At 1212 h, the intestines and contents were all that remained and the orang-utan moved to another tree nearby and started eating leaves. He continued eating leaves until 1236 h, and then proceeded to travel through the forest in a westerly direction again.

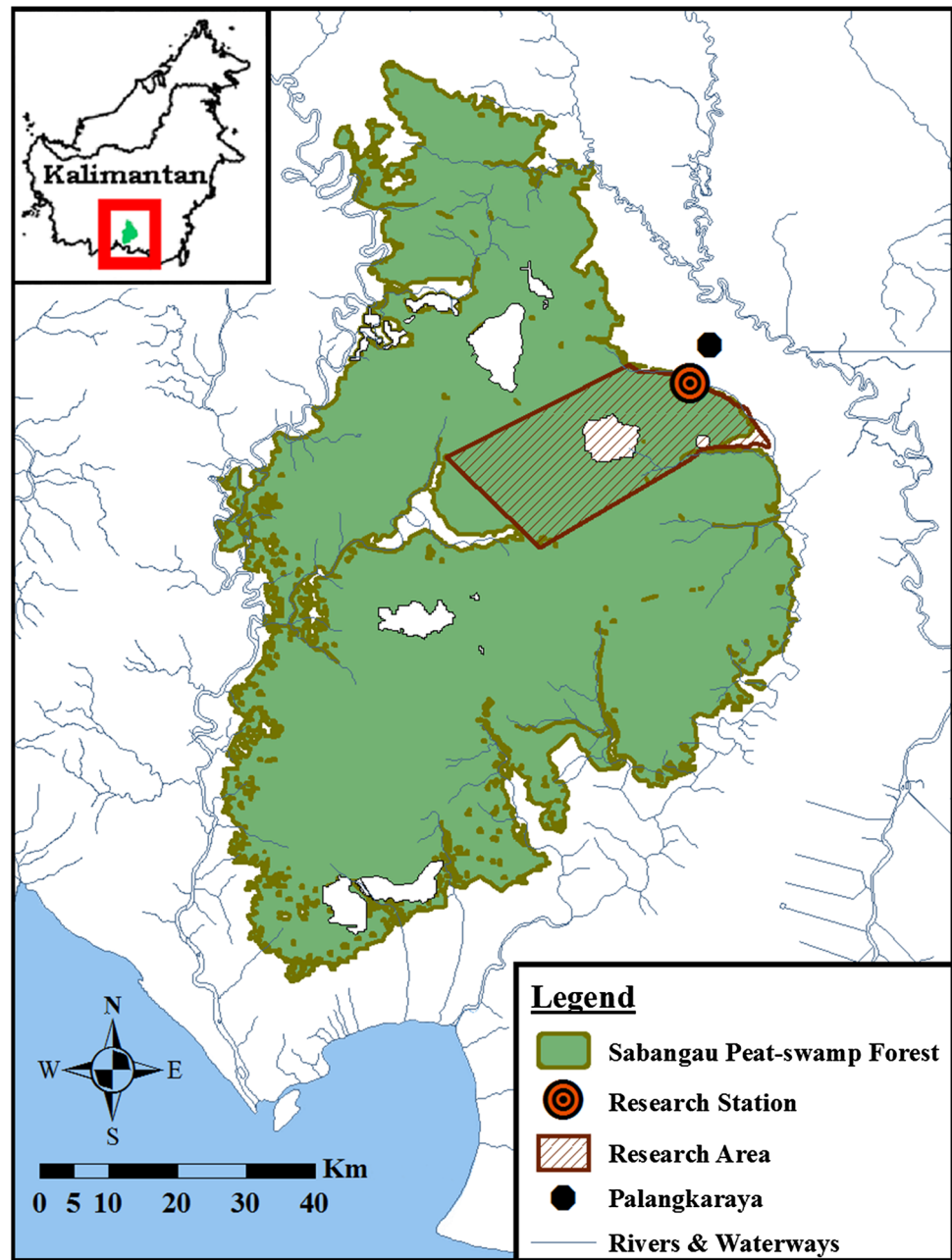
No other orang-utans or other primates were observed in the area during this event.

Discussion

Eating of vertebrate meat by Bornean orang-utans (*Pongo pygmaeus*) is a very rare occurrence. In 2200 days of follows of 55 individuals between 2003 and 2012 (over 16,000 h of observations) in Sabangau by H.C.M.-B. and colleagues, no observation of an orang-utan eating a vertebrate has previously been witnessed. This is the first fully documented observation of meat-eating by an orang-utan in Borneo.

Whilst previous accounts of meat-eating by Sumatran orang-utans (*P. abelii*) are described as opportunistic (Utami and van Hooff 1997), in all cases the prey was seized and killed by the orang-utan. Hardus et al. (2012) describe the orang-utans making abrupt diversions to their direction of travel within 40 m of the slow-loris capture, and returning to their original travel path at the end of the feeding bout, which can be interpreted as a meaningful intention to catch the loris; the hunting process appears to follow a set pattern where the orang-utan stuns the loris by hitting it, either grabs the body directly or moves to the ground to retrieve it, if it has fallen from the tree, and kills it by biting the head (Utami and van Hooff 1997; Hardus et al. 2012). In the observation of this Bornean male, there was no discernible change in the orang-utan's travel direction, either before or after the meat-eating event (Fig. 3); no chase occurred, and the orang-utan did not come to the ground to retrieve the prey. Unlike slow lorises, horse-tailed squirrels are diurnal, and usually travel and feed in small trees in the lower and middle understorey and occasionally on the ground (Payne et al. 1985; Haslauer 2010). Few predators can chase and capture adult horse-tailed squirrels, as they are agile climbers and rely on

Fig. 1 Map of the Sabangau Forest ecosystem, with the Natural Laboratory of Peat Swamp Forest (research area) highlighted. Adapted from Ehlers Smith and Ehlers Smith (2013)



this agility and vigilance to avoid predation (Payne et al. 1985; Haslauer 2010). Thus, it is unlikely that a male orang-utan would be capable of chasing and catching a healthy adult horse-tailed squirrel. Combined with the lack of squealing and lack of blood on the carcass, this would suggest the orang-utan obtained this squirrel by scavenging rather than hunting and killing, although we cannot rule out the possibility that the squirrel was alive when first obtained by the orang-utan. There are few reports of scavenging by non-human primates (Butynski 1982b), and scavenging by an orang-utan is described in only one published report: Sugardjito and Nurhuda (1981) observed

a Sumatran female eating a carcass in Ketambe. Although their account is now believed to be another instance of capture and consumption of a slow loris (Rijksen and Meijaard 1999; Hardus et al. 2012), our observation provides further evidence that, albeit rarely, orang-utans may scavenge meat. This event adds a new important record to the brief catalogue of reports on scavenging by non-human primates.

The male orang-utan repeatedly turned his back on the observers in the early stages of the feeding bout, which mirrors the behaviour of adult Sumatran females towards their offspring when feeding on slow loris meat. They

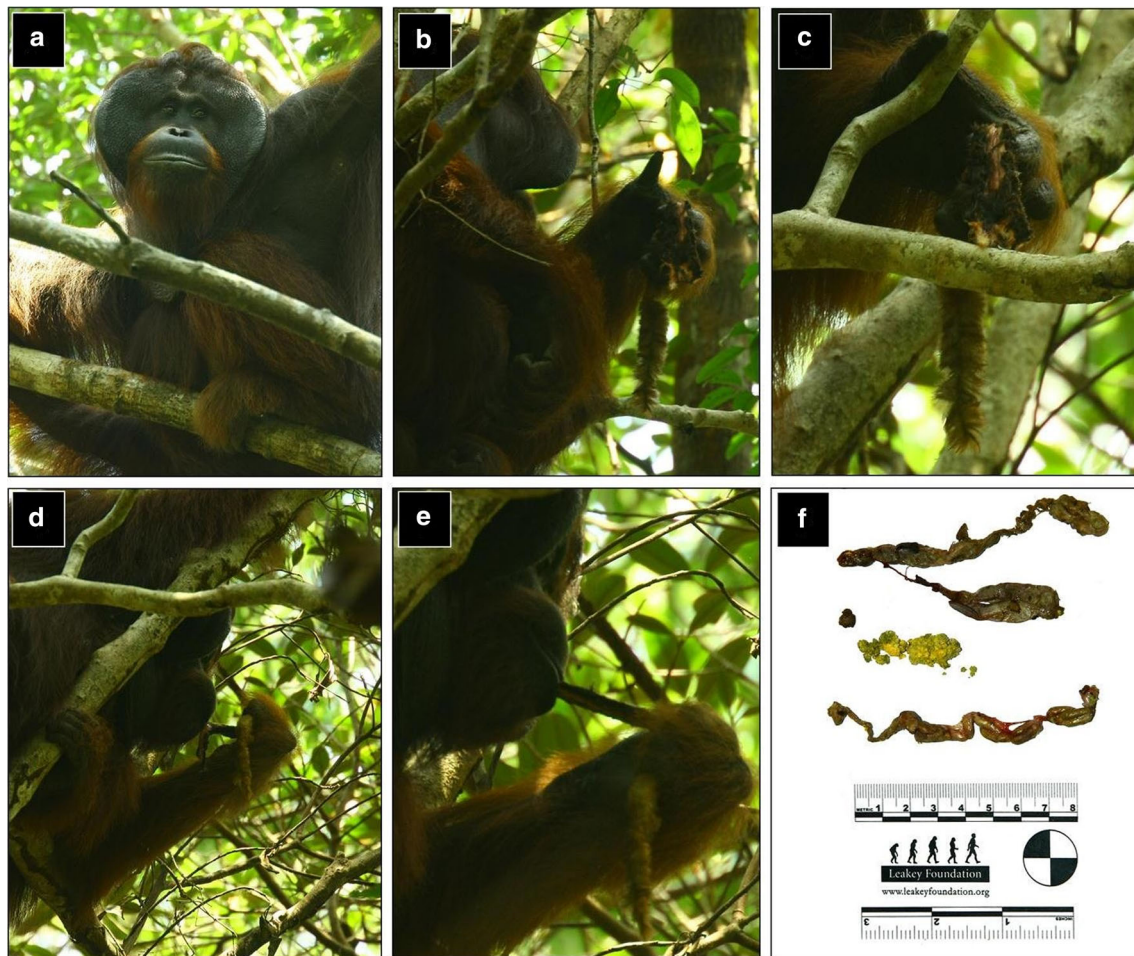


Fig. 2 **a** The subject of this observation, a wild, unhabituated adult flanged male orang-utan. **b, c** First clear view of the meat-eating behaviour. **d, e** The orang-utan was observed pulling the carcass

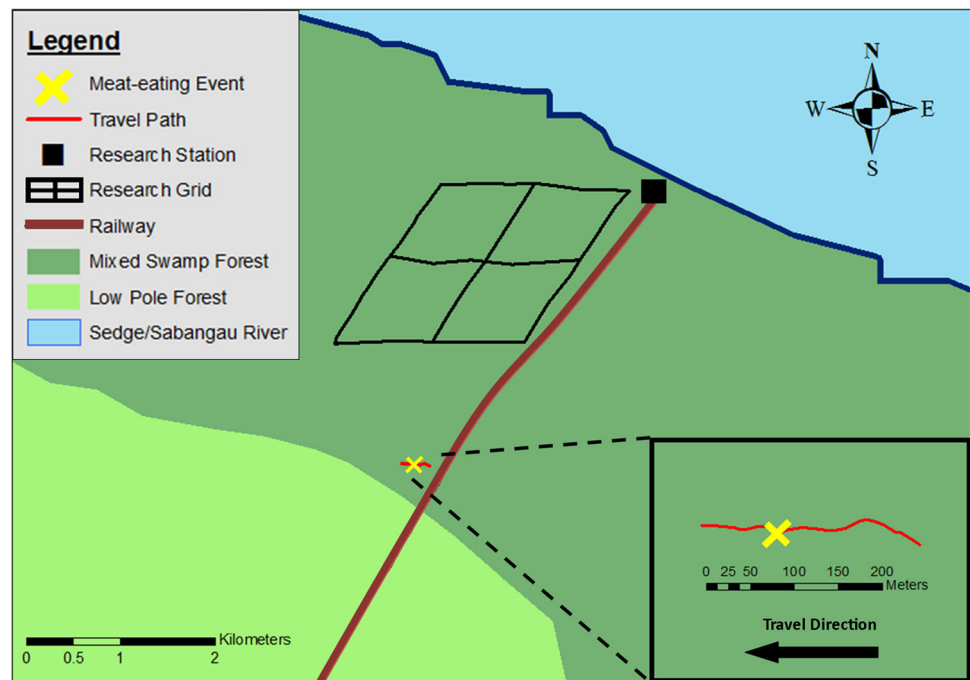
through his teeth. **f** The intestines and contents were the only remains of the squirrel carcass after the feeding bout. All photographs © Ben Buckley 2012

actively resist food-sharing by turning their backs or slapping the offspring (Utami and van Hooff 1997). The head of the squirrel was missing by the time full observation of the carcass was possible. This is consistent with the feeding pattern observed in Sumatran orang-utans eating loris carcasses, in which the head is invariably eaten first (Utami and van Hooff 1997; Hardus et al. 2012). The squirrel carcass was not observed before the orang-utan started eating it, however, so it is possible that the head was already missing before the carcass was acquired. In three observations of Sumatran orang-utans eating fresh-caught slow loris in 2007 and 2008, feeding times ranged from 140 to 244 min (Hardus et al. 2012), but, in this event, the Bornean male fed on the squirrel carcass for just 41 min. Horse-tailed squirrels are generally smaller than slow lorises, with bodyweight of 260–365 g for horse-tailed squirrel compared with 230–610 g for slow loris (Payne et al. 1985); nevertheless, it would seem that the Bornean male in our observation may have consumed the squirrel

carcass at a faster rate than previously observed in other meat-eating orang-utans. In the Sumatran cases, either all parts of the carcass were consumed or small pieces of skin or bone remained at the end of the feeding bout (Utami and van Hooff 1997; Hardus et al. 2012); in the case reported here, some intestines were dropped during the feeding bout, but no skin or bone remained at the end. The speed and efficiency with which the orang-utan devoured the carcass may indicate prior experience of eating vertebrate meat, but the deduction that this may have been an act of scavenging rather than hunting would point to it being a chance event.

This observation took place 1.5 km deeper into the forest than all previous orang-utan follows, in a transitional habitat between the relatively high-productivity mixed-swamp forest and the lower-productivity low-pole forest (Fig. 3; see Page et al. 1999 for habitat sub-type descriptions). Orang-utan densities are twice as high in mixed swamp forest than in the low-pole forest (Morrogh-Bernard

Fig. 3 Map of a section of the Natural Laboratory of Peat Swamp Forest showing the research station, the travel path and direction of the Bornean male orang-utan during this observation and the location of the meat-eating event



et al. 2003). It is possible that presumed lower food availability in this habitat had an influence on this individual's choice of diet. In Sumatra, a correlation between low fruit availability, especially low ripe-fruit availability, and increased slow-loris eating suggests that loris may be considered a filler fallback food for Sumatran orang-utans (Hardus et al. 2012). During the month in which this event was observed, August 2012, the fruit availability of known orang-utan food species was higher than the other months of 2012, and also higher than 68 % of all months between 2003 and 2012. As such, low food availability, in this instance, cannot be the reason why this behaviour occurred.

Nevertheless, opportunistic experimentation with novel food sources is likely to be an important survival mechanism during periods of food scarcity and extreme negative energy balance. In a study on feeding behaviour in the mixed peat-swamp forest at Sabangau, Harrison (2009) showed that flanged males have the highest daily metabolisable energy intake of all the age–sex classes, and yet their energy intake was still markedly lower than the estimated energy expenditure (based on Knott 1999b) for their class in all months of the study. Although there were no significant differences in overall diet composition between the different age–sex classes, flanged males had lower energy intake during periods of low fruit and flower availability, and obtained significantly more of their energy from protein sources during these periods (see Harrison 2009). Thus, it is possible that the negative energy balance experienced by flanged males at Sabangau, especially during periods/in areas of low fruit availability, contributed

to the attractiveness of squirrel meat as a food source for this individual. Although the peat swamps of Sabangau are reckoned to be a low-productivity habitat, with consequent frequent periods of negative energy balance in its orang-utans (Harrison et al. 2010), energetic stress is unlikely to be the sole driving factor behind this incident, given the high frequency of observed negative energy balance across the orang-utan population and the extreme rarity of meat-eating events.

All but one of the previous reports of meat-eating by orang-utans involve adult females; this contrasts with vertebrate hunting in other primate species, in which males are the predominant hunters. The female bias in vertebrate capture among orang-utans may be because females spend longer than males foraging for insects, and it is during these foraging periods that lorises are encountered (van Schaik et al. 2009). In Ketambe, Sumatra, in 40 years of behavioural research, almost all observations of meat-eating are limited to a single wild adult female and her infant (van Schaik et al. 2009; Hardus et al. 2012), highlighting the individuality of diet choice. Orang-utans who have been observed to catch lorises appear to be adept and experienced at it, and there is only one report of an orang-utan failing to acquire prey that it was hunting, when a female in Suaq Balimbing successfully slapped a slow loris out of a tree, but then failed to retrieve it on the ground (Hardus et al. 2012). Thus, it has been suggested that orang-utan predation may be an idiosyncratic trait (Utami and van Hooft 1997) or a cultural behaviour (van Schaik et al. 2003), as an explanation for why certain individuals

show habitual hunting behaviour, whilst others in the same population do not.

In the wider context of primate diets, meat-eating behaviour is found to vary widely between ape species. Active-pursuit hunting for meat is reported from all studied populations of chimpanzees (*Pan troglodytes* spp.) preying on 32 species of mammal (Goodall 1968; McGrew 1983; Boesch and Boesch 1989; Uehara 1997; Mitani and Watts 2001). A group of wild black-crested gibbons (*Nomascus concolor jingdongensis*) have been observed to attack, kill and eat giant flying squirrels on four occasions in China (Fan and Jiang 2009). Instances of opportunistic hunting have been observed in bonobos (*Pan paniscus*), preying on flying squirrels, monkeys and duiker (Badrian and Malenky 1984; Ihobe 1992; Surbeck and Hohmann 2008). Gorillas (*Gorilla* spp.) are known to eat insects (Tutin and Fernandez 1992), but are not generally considered to eat vertebrate meat in the wild. Amongst monkey species, meat-eating is also prevalent in populations of baboons (*Papio* spp.; Altmann and Altmann 1970; Harding 1975; Strum 1975, 1983), capuchins (*Cebus* spp.; Fedigan 1990) and vervet monkeys (*Cercopithecus aethiops*; Struhsaker 1967; Kavanagh 1978), and reported occasionally in blue monkeys (*Cercopithecus mitis*; Butynski 1982a), among others. These species adopt an opportunistic strategy of simply grabbing the prey or chasing it for a short distance, similar to that of Sumatran orang-utans, in contrast to the strategic co-operative pursuit employed by chimpanzees (Teleki 1975).

The other primate species in which hunting is recorded are all group-living species in which meat sharing with unrelated individuals could lead to mating advantage, proposed as the meat-for-sex hypothesis (Mitani and Watts 2001; Stanford et al. 1994a; Teleki 1973). This is unlikely to play a role in orang-utan meat-eating behaviour: in no observed instances of slow-loris capture did the individual share the meat with unrelated individuals (Utami and van Hoof 1997). Hunting in chimpanzees is predominantly a male activity (McGrew 1992) and is attributed to the male-social-bonding hypothesis (Mitani and Watts 2001; Mitani et al. 2002; Takahata et al. 1984); but this male bias may be absent when meat acquisition is more opportunistic, such as seizing small ungulates, e.g. blue duiker (*Philantomba monticola*), bushbuck fawns (*Tragelaphus scriptus*) (Takahata et al. 1984; Uehara et al. 1992) or bushbaby (*Galago senegalensis*; Pruett and Bertolani 2007). Due to the semi-solitary nature of orang-utans, social-learning opportunities are limited compared with other primate species, but on Sumatra females are more gregarious, and party sizes of females at Suaq Balimbing are comparable to those of female forest chimpanzees (van Schaik 1999; Wich et al. 1999). This may contribute to the female bias seen in loris-hunting behaviour (van Schaik et al. 2009).

Scavenging by wild non-human primates is uncommon, and in cases where it occurs it is almost exclusively limited to carcasses which are fresh (Butynski 1982b; Ragir et al. 2000). It is suggested that, within primates, carrion avoidance is a dietary strategy developed in response to experiences of gastro-intestinal disease associated with contaminated meat (Ragir et al. 2000). The extreme rarity of observations of meat-eating and scavenging events in orang-utans means that vertebrate meat cannot be considered a normal part of their diet, and as such it may be that learned avoidance behaviours are absent from a species that eats meat so infrequently. As noted by Russon et al. (2009), however, the increasing evidence that different populations of wild orang-utans eat meat, albeit rarely, points to this behaviour being a feature common to the great apes and not one that emerged in a more recent ancestor of *Homo* and *Pan*.

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References

- Altmann SA, Altmann J (1970) Baboon ecology: African field research. University of Chicago Press, Chicago
- Badrian N, Malenky RK (1984) Feeding ecology of *Pan paniscus* in the Lomako Forest, Zaire. In: Susman RL (ed) The pygmy chimpanzee: evolutionary biology and behavior. Plenum, New York, pp 275–299
- Boesch C, Boesch H (1989) Hunting behavior of wild chimpanzees in the Tai National Park. *Am J Phys Anthropol* 78:547–573
- Butynski TM (1982a) Blue monkey (*Cercopithecus mitis stuhlmanni*) predation on galagos. *Primates* 23:563–566
- Butynski TM (1982b) Vertebrate predation by primates: a review of hunting patterns and prey. *J Hum Evol* 11:421–430
- Dale S (1986) Saving and studying orangutans of Borneo. *Chicago Tribune* (Internet). http://articles.chicagotribune.com/1986-04-06/travel/8601250280_1_orangutan-rod-brindamour-rain-forest. Accessed 15 Jan 2014
- Ehlers Smith DA, Ehlers Smith YC (2013) Population density of red langurs in Sabangau tropical peat-swamp forest, Central Kalimantan, Indonesia. *Am J Primatol* 75:837–847
- Fan P, Jiang X (2009) Predation on giant flying squirrels (*Petaurista philippensis*) by black crested gibbons (*Nomascus concolor jingdongensis*) at Mt. Wuliang, Yunnan, China. *Primates* 50:45–49
- Fedigan LM (1990) Vertebrate predation in *Cebus capucinus*: meat eating in a Neotropical monkey. *Folia Primatol* 54:196–205
- Goodall J (1968) The behaviour of free-living chimpanzees in the Gombe Stream Reserve. Baillière, Tindall and Cassell, London
- Harding RSO (1975) Meat-eating and hunting in baboons. In: Tuttle R (ed) Socioecology and psychology of primates. Mouton, The Hague, pp 245–257
- Hardus ME, Lameira AR, Zulfa A, Utami Atmoko SS, de Vries H, Wich SA (2012) Behavioral, ecological, and evolutionary

- aspects of meat-eating by Sumatran orangutans (*Pongo abelii*). *Int J Primatol* 33:1–18
- Harrison ME (2009) Orang-utan feeding behaviour in Sabangau. PhD thesis, University of Cambridge, Cambridge (unpublished)
- Harrison ME, Morrogh-Bernard HC, Chivers DJ (2010) Orangutan energetics and the influence of fruit availability in the nonmasting peat-swamp forest of Sabangau, Indonesian Borneo. *Int J Primatol* 31:585–607
- Haslauer R (2010) *Sundasciurus hippurus* (horse-tailed squirrel) (Online), Animal Diversity Web http://animaldiversity.org/accounts/Sundasciurus_hippurus. Accessed 09 July 2015
- Ihobe H (1992) Observations on the meat-eating behavior of wild bonobos (*Pan paniscus*) at Wamba, Republic of Zaire. *Primates* 33:247–250
- Kavanagh M (1978) The diet and feeding behaviour of *Cercopithecus aethiops tantalus*. *Folia Primatol* 30:30–63
- Knott CD (1999a) Orangutan behavior and ecology. In: Dolhinov P, Fuentes A (eds) *The nonhuman primates*. Mayfield, Mountain View, pp 50–57
- Knott CD (1999b) Reproductive, physiological and behavioral responses of orangutans in Borneo to fluctuations in food availability. PhD thesis, Harvard University, Cambridge, Massachusetts (unpublished)
- McGrew WC (1983) Animal foods in the diets of wild chimpanzees (*Pan troglodytes*): why cross-cultural variation? *J Ethol* 1:46–61
- McGrew WC (1992) Chimpanzee material culture. Implications for human evolution. Cambridge University Press, Cambridge
- Mitani JC, Watts DP (2001) Why do chimpanzees hunt and share meat? *Anim Behav* 61:915–924
- Mitani JC, Watts DP, Muller MN (2002) Recent developments in the study of wild chimpanzee behavior. *Evol Anthropol Issues News Rev* 11:9–25
- Morrogh-Bernard H, Husson S, Page SE, Rieley JO (2003) Population status of the Bornean orang-utan (*Pongo pygmaeus*) in the Sebangau peat swamp forest, Central Kalimantan, Indonesia. *Biol Conserv* 110:141–152
- Page SE, Rieley JO, Shotyck W, Weiss D (1999) Interdependence of peat and vegetation in a tropical peat swamp forest. *Philos Trans R Soc Lond B Biol Sci* 354:1885–1897
- Payne J, Francis CM, Phillipps K (1985) *A field guide to the mammals of Borneo*. Sabah Society, Kota Kinabalu; and World Wildlife Fund Malaysia, Kuala Lumpur
- Pruetz JD, Bertolani P (2007) Savanna chimpanzees, *Pan troglodytes verus*, hunt with tools. *Curr Biol* 17:412–417
- Ragir S, Rosenberg M, Tierno P (2000) Gut morphology and the avoidance of carrion among chimpanzees, baboons, and early hominids. *J Anthropol Res* 56:477–512
- Rijksen HD, Meijaard E (1999) *Our vanishing relative: the status of wild orang-utans at the close of the twentieth century*. Kluwer Academic, Dordrecht
- Russon AE, Wich SA, Ancrenaz M, Kanamori T, Knott CD, Kuze N, Morrogh-Bernard HC, Pratje P, Ramlee H, Rodman P, Sawang A, Sidiyasa K, Singleton I, van Schaik CP (2009) Geographic variation in orangutan diets. In: Wich SA, Utami Atmoko SS, Mitra Setia T, van Schaik CP (eds). *Orangutans: geographic variation in behavioral ecology and conservation*. Oxford University Press, Oxford. pp 135–156
- Stanford CB, Wallis J, Mpongo E, Goodall J (1994) Hunting decisions in wild chimpanzees. *Behaviour* 131:1–18
- Struhsaker TT (1967) Ecology of vervet monkeys (*Cercopithecus aethiops*) in the Masai–Amboseli Game Reserve, Kenya. *Ecology* 48:892–904
- Strum SC (1975) Primate predation: interim report on the development of a tradition in a troop of olive baboons. *Science* 187:755
- Strum SC (1983) Baboon cues for eating meat. *J Hum Evol* 12:327–336
- Sugardjito J, Nurhuda N (1981) Meat-eating behaviour in wild orangutans, *Pongo pygmaeus*. *Primates* 22:414–416
- Surbeck M, Hohmann G (2008) Primate hunting by bonobos at LuiKotale, Salonga National Park. *Curr Biol* 18:906–907
- Takahata Y, Hasegawa T, Nishida T (1984) Chimpanzee predation in the Mahale Mountains from August 1979 to May 1982. *Int J Primatol* 5:213–233
- Teleki G (1973) *The predatory behavior of wild chimpanzees*. Bucknell University Press, Lewisburg
- Teleki G (1975) Primate subsistence patterns: collector-predators and gatherer-hunters. *J Hum Evol* 4:125–184
- Tutin CEG, Fernandez M (1992) Insect-eating by sympatric lowland gorillas (*Gorilla g. gorilla*) and chimpanzees (*Pan t. troglodytes*) in the Lopé Reserve, Gabon. *Am J Primatol* 28:29–40
- Uehara S (1997) Predation on mammals by the chimpanzee (*Pan troglodytes*). *Primates* 38:193–214
- Uehara S, Nishida T, Hamai M, Hasegawa T, Hayaki H, Huffman MA, Kawanaka K, Kobayashi S, Mitani JC, Takahata Y, Takasaki H, Tsukahara T (1992) Characteristics of predation by the chimpanzees in the Mahale Mountains National Park, Tanzania. *Top Primatol* 1:143–158
- Utami SS, van Hooff JA (1997) Meat-eating by adult female Sumatran orangutans (*Pongo pygmaeus abelii*). *Am J Primatol* 43:159–165
- van Schaik CP (1999) The socioecology of fission-fusion sociality in orang-utans. *Primates* 40:69–86
- van Schaik CP, Ancrenaz M, Borgen G, Galdikas B, Knott CD, Singleton I, Suzuki A, Utami SS, Merrill M (2003) Orangutan cultures and the evolution of material culture. *Science* 299:102
- van Schaik CP, van Noordwijk MA, Vogel ER (2009) Ecological sex differences in wild orangutans. In: Wich SA, Utami Atmoko SS, Mitra Setia T, van Schaik CP (eds) *Orangutans: geographic variation in behavioral ecology and conservation*. Oxford University Press, Oxford. pp 255–268
- Wich SA, Sterck H, Utami SS (1999) Are orang-utan females as solitary as chimpanzee females? *Folia Primatol* 70:23–28
- Wich SA, Meijaard E, Marshall AJ, Husson S, Ancrenaz M, Lacy RC, van Schaik CP, Sugardjito J, Simorangkir T, Traylor-Holzer K, 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