Orangutan diet: lessons from and for the wild
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Behavioral, Ecological, and Evolutionary Aspects of Meat-Eating by Sumatran Orangutans (*Pongo abelii*)

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Abstract
Meat-eating is an important aspect of human evolution, but how meat became a substantial component of the human diet is still poorly understood. Meat eating in our closest relatives, the great apes, may provide insight into the emergence of this trait, but most existing data are for chimpanzees. We report 3 rare cases of meat-eating of slow lorises, *Nycticebus coucang*, by 1 Sumatran orangutan mother–infant dyad in Ketambe, Indonesia, to examine how orangutans find slow lorises and share meat. We combine these 3 cases with 2 previous ones to test the hypothesis that slow loris captures by orangutans are seasonal and dependent on fruit availability. We also provide the first (to our knowledge) quantitative data and high-definition video recordings of meat chewing rates by great apes, which we use to estimate the minimum time necessary for a female *Australopithecus africanus* to reach its daily energy requirements when feeding partially on raw meat. Captures seemed to be opportunistic but orangutans may have used olfactory cues to detect the prey. The mother often rejected meat sharing requests and only the infant initiated meat sharing. Slow loris captures occurred only during low ripe fruit availability, suggesting that meat may represent a filler fallback food for orangutans. Orangutans ate meat more than twice as slowly as chimpanzees (*Pan troglodytes*), suggesting that group living may function as a

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meat intake accelerator in hominoids. Using orangutan data as a model, time spent chewing per day would not require an excessive amount of time for our social ancestors (australopithecines and hominids), as long as meat represented no more than a quarter of their diet.

Introduction
It is generally assumed that in early humans, a calorie-rich, meat-based diet became available through an evolving kit of hunting tools and/or techniques (Richards, 2002). However, Wrangham and colleagues suggest, that the shift to a meat-based diet in the human lineage may have been impossible without the knowledge of cooking (Wrangham & Carmody, 2010; Wrangham & Conklin-Brittain, 2003; Wrangham, 2009). Using chimpanzees as a model, Wrangham and Conklin-Brittain (2003) calculated that an early hominin with daily energy requirements of maximum 2487 kcal per day (Aiello & Key, 2002) would have had to spend 50% of a 12-hour day chewing raw meat. This is a significant period for chewing per day, since individuals must engage in other activities, and Wrangham and Conklin-Brittain (2003) used these results to support the hypothesis that early humans must have had a technique to tenderize meat, that is, cooking, for meat to become an important part of their diet.

At present, humans consume an average of 40kg of meat per capita per year, with several countries reaching more than 100kg of meat per capita per year (FAOSTAT, 2011). Indeed, humans may rely entirely on meat in certain times of the year (e.g. Iglulik Central Eskimos in winter; Sinclair, 1953). Vertebrate meat-eating is also practiced by a number of non-human primates such as capuchins (Cebus sp.; Rose, 1997) and baboons (Papio anubis; Strum, 1983), in which males typically capture the prey (Rose, 1997; Stanford, 1999; Strum, 1983; Uehara, 1997; Wrangham & van Zinnicq Bergmann Riss, 1990). In great apes, meat-eating occurs in chimpanzees (Pan troglodytes; e.g. Boesch & Boesch, 1989), bonobos (Pan paniscus; Hohmann & Fruth, 2008) and Sumatran orangutans (Pongo abelii; Utami & Van Hooff, 1997). However, in contrast to humans, the diets of great apes are primarily composed of fruits and other plant foods. Currently, evidence concerning the social and ecological conditions favoring meat-eating in great apes is scant, with the exception of data for chimpanzees (e.g. Gilby & Wrangham, 2007; Gilby et al., 2006; Gilby et al., 2010; Mitani & Watts, 2005; Watts & Mitani, 2002). For chimpanzees, researchers have proposed 5 hypotheses: the fallback food hypothesis (nutrient shortfall hypothesis), meat-for-sex
hypothesis, the nutrient surplus hypothesis, male social bonding hypothesis and increased visibility hypothesis. There is no evidence to support the fallback food hypothesis, under which meat-eating is predicted to occur during periods of food scarcity (Gilby et al., 2006). Hunting frequency was highest during dry season (Stanford et al., 1994b), but it was unclear if food scarcity caused this trend (Gilby et al., 2006). Equally, there is no evidence for the meat-for-sex hypothesis, whereby meat is exchanged for matings (Gilby, 2006; Gilby et al., 2006; Gilby et al., 2010). However, there is some evidence in favor of the nutrient surplus hypothesis, wherein hunts are more frequent when energy reserves are high (e.g. Gilby et al., 2006). At least 3 studies have shown that chimpanzees hunt more when ripe fruit is abundant (Gilby & Wrangham, 2007; Gilby et al., 2006; Mitani & Watts, 2005). At Gombe (Gilby et al., 2006) and Ngogo (Mitani & Watts, 2005) this pattern is the result of increased group size when fruit is abundant, supporting the male bonding hypothesis (Hosaka et al., 2001; Mitani & Watts, 2001; Stanford et al., 1994a), whereas at Kanyawara, the positive effect of fruit abundance on hunting probability remains even after group size is controlled (Gilby & Wrangham, 2007). Another ecological factor that has been found to influence meat-eating in chimpanzees is increased visibility. Chimpanzees hunt more in woodland and semi-deciduous forest compared to evergreen forest (Gilby et al., 2006), and in areas where canopy is broken and/or with secondary growth (Watts & Mitani, 2002).

Researchers have observed several cases of meat-eating in wild Sumatran orangutans, although not in Bornean orangutans (Pongo pygmeus; Russon et al., 2009). However, meat-eating is rare at the Sumatran orangutan sites where this behavior has been observed despite numerous observation hours (van Schaik et al., 2003). The available data suggest that unlike other primate species, orangutans do not show a male bias in meat-eating (van Schaik et al., 2009b). However, a male bias may also be absent in chimpanzees for more opportunistic prey, such as bushbabies (species not reported; Pruetz & Bertolani, 2007) and bushbuck fawns (Tragelaphus scriptus; I.C. Gilby, pers. comm.). Slow loris hunting has previously been observed in 2 adult female orangutans in the Ketambe population (Utami & Van Hooff, 1997), and in 3 individuals (2 adult females and 1 flanged male) at Suaq Balimbing (van Schaik et al., 2009b). These studies reported a total of 9 cases of orangutans eating slow lorises (Utami & Van Hooff, 1997; van Schaik et al., 2009b). A further case of an orangutan eating a gibbon (Sugardjito & Nurhuda, 1981) is also likely to have in fact involved a slow loris (Rijksen & Meijaard, 1999). Recently, we observed 3 new cases of meat-eating and recorded details of the meat-eating from prey discovery until the end of
prey consumption, including, to our knowledge, the first video recording of the behavior (http://www.springerlink.com/content/l0735364k211482x/supplementals/). We present these data, complemented with those of previous orangutan meat-eating observations where relevant data are available, and use these data to examine how orangutans find slow lorises and share meat. We also examine when and why orangutans eat meat in light of the hypotheses proposed to explain meat-eating in chimpanzees.

The hypothesis of increased visibility is not applicable to orangutans because they inhabit tropical rainforest with continuous dense canopy throughout dry and wet seasons. However, seasonal variations in high quality foods may elicit meat hunting. Because previous cases were not reported during mast years (Utami & Van Hooff, 1997), they may suggest that the seasonal shortage of food elicits a need for fallback foods in the form of meat (Boesch & Boesch-Achermann, 2000; Mitani & Watts, 2005; Rose, 1997, 2001; Stanford, 1996; Teleki, 1973). Accordingly, we test whether meat-eating is negatively correlated with fruit availability.

Finally, we calculate meat chewing rates, and grams and calories consumed per hour for orangutans and use these to estimate the minimum time necessary for a female Australopithecus africanus to reach its daily energy requirements when feeding partially on raw meat. Orangutans have more robust jaws than early humans and are more similar in their dentition to australopithecines than to Homo erectus (Grine & Kay, 1988). Some australopithecines are suggested to have relied on fruits and their fallback food may have been harder, tougher (or granular) than fruit (Teaford et al., 2002). As this is also the case for orangutans in comparison with chimpanzees (Vogel et al., 2008), whose dentition is more similar to that of Homo erectus (Wood, 1995), orangutans are a useful model in this context.
Methods
We conducted this study at the Ketambe Research Station, Gunung Leuser National Park, Leuser Ecosystem, Sumatra, Indonesia (3°41’ N, 97°39’ E) between November 2006 and October 2008. The Ketambe research area consists mainly of primary rainforest (Rijksen, 1978; van Schaik & Mirmanto, 1985) and selectively logged forest. All 3 recent cases involved 1 adult female orangutan (Yet) and her dependent female offspring (Yeni, born in 2001) and occurred in February and December 2007 and in April 2008 (Table 1). We refer to Yeni as an infant because she was not yet fully weaned at the age of 6-7 years (van Noordwijk & van Schaik, 2005; Wich et al., 2004b). She was the only individual accompanying her mother during the observed cases of slow loris hunting.

M.E.Hardus, A.Zulfa, and experienced local field assistants observed these new cases during focal follow days (i.e. observations on an orangutan individual, whenever possible from morning nest until evening nest). We collected standardized observational data during each follow day (van Schaik, 1999; www.aim.unizh.ch/orangutannetwork.html), comprising feeding time, food species and items, feeding technique and social interactions between mother-infant and other orangutans. In addition, we drew orangutans’ travel path on GPS-constructed maps of the research area, noting the location of each feeding bout. M.E.Hardus collected meat chewing rates during the slow loris case of December 2007, and
insects and leaves chewing rates between April 2007 and January 2008 via video recordings using a Sony HDV 1080i camera with a Manfrotto monopod.

We define food sharing as a transfer of a food item from one individual to another (Feistner & McGrew, 1989). We define active sharing as the mother giving food to her begging infant instead of allowing it to take the food (passively tolerant), and active resistance as the mother not letting go of a food item, taking the food out of her infant’s hand, and/or turning her back towards her infant (de Waal, 1989; Jaeggi et al., 2008).

Experienced assistants recorded fruit availability data monthly from phenology plots (for details see van Schaik, 1986; Wich & van Schaik, 2000). During 1993-4 data on fruit availability was standardized by computing z-scores due to differences in methods and observers (Wich & van Schaik, 2000). During 2006-8 we calculated fruit availability as the percentage of trees carrying fruits or ripe fruits. We treated these 2 observation periods separately because of these differences.

We developed a Monte Carlo test procedure, written in R version 2.13.0 (R Development Core Team, 2011), to test the null hypothesis that slow loris eating occurred independently of fruit availability (or ripe fruit availability). We explain this method here using the data set collected in the period November 2006 – September 2008. In this period researchers observed the orangutan mother and infant for 916 follow hours, during which 3 cases of slow loris eating occurred. First, we constructed a frequency histogram showing the distribution of number of follow hours for the different observed fruit availabilities (Figure 2a). Next, we randomly drew 3 observations of fruit availability according to this frequency distribution, and calculated the mean of these three randomly chosen fruit availabilities. We repeated this random drawing of sets of 3 observed fruit availabilities 10000 times, yielding a null frequency distribution of average fruit availabilities (Figure 2b). Next, we calculated the observed average percentage of fruit availability at the time of slow loris eating (2.38 + 2.13 + 5.14)/5 =3.22, and compared this against the null distribution.

We calculated the left tailed significance level ($P_l$) of the observed mean value of 3.22 under the null hypothesis that the slow loris eating occurred independently of the fruit availability in the following way. For each of the 10,000 Monte Carlo replications, we compared the observed value 3.22 to the random value. If the random value was “less than or equal to” (i.e. LTEQ) the observed value 3.22, we increased a LTEQ counter by 1. We then calculated $P_l$ as (LTEQ+1)/(10,000+1). (The +1 in the numerator and denominator is to
ensure that $P_l$ is greater than 0.) Because we only look at the left-tailed probability we set the critical probability level at 0.025.

We used the same Monte Carlo test procedure to test whether slow loris meat-eating occurred independently of the availability of ripe fruit. We used data from January 1993 – December 1994 (Period A; Figure 3a), in which we observed 2 cases of slow loris eating; and for November 2006 – September 2008 (Period B; Figure 3b), in which we observed 3 cases of slow loris eating. For period A we calculated the random mean values from 2 randomly drawn observed fruit availabilities, while for period B we based these random mean values on 3 randomly drawn observed fruit availabilities (as explained above). Unfortunately, observers did not record the number of follow hours from June 1991 – December 1992, so we could not use data collected during this period although 1 case of slow loris eating was observed in February 1992.

Finally, we performed a Monte Carlo test in which we combined period A and B. Because researchers used different methods for assessing fruit availability in the two periods, we could not combine the data for the 5 cases of slow loris eating that occurred during this whole period. Instead, we performed the Monte Carlo test for both periods simultaneously and calculated a combined left tailed significance level ($P_l$) in the following way: For each of the 10,000 Monte Carlo replications, we compared the observed value of 8.00 in period A to the random value for period A and simultaneously compared the observed value of 3.22 in period B to the random value for period B. If the random value in period A was less than or equal to the observed value 8.00 and the random value in period B was also less than or equal to the observed value of 3.22, we increased a LTEQAB counter by 1. $P_l$ was then equal to (LTEQAB+1)/(10,000+1). For instance, if $P_l = 0.01$, then the chance of observing a mean fruit availability of 8.00 or less in period A and also observing a mean fruit availability of 3.22 or less in period B, under the null hypothesis that these 2 and 3 fruit availabilities are randomly distributed, was 1%.
Table 1. Slow loris captures by Sumatran orangutans at Ketambe research station

| # | Year | Month | Data available                                      | Reference            |
|---|------|-------|-----------------------------------------------------|----------------------|
| 1 | 1989 | -     | location                                            | Utami & van Hooff (1997) |
| 2 | 1989 | -     | location                                            | Utami & van Hooff (1997) |
| 3 | 1989 | -     | location                                            | Utami & van Hooff (1997) |
| 4 | 1992 | Feb.  | location, food availability                         | Utami & van Hooff (1997) |
| 5 | 1993 | Apr.  | location, food availability                         | Utami & van Hooff (1997) |
| 6 | 1994 | Feb.  | location, food availability                         | Utami & van Hooff (1997) |
| 7 | 2007 | Feb.  | location, food availability, duration, feeding rate, meat sharing | this study |
| 8 | 2007 | Dec.  | location, food availability, duration, feeding rate, meat sharing, chewing rates | this study |
| 9 | 2008 | Apr.  | location, food availability, duration, feeding rate | this study |

Figure 2a (left). Frequency histogram showing the distribution of number of follow hours of Yet for the various observed fruit availabilities in 2006-2008. Figure 2b (right). Frequency
Results

Behavioral data
All 9 observed cases of slow loris-eating at Ketambe occurred at different locations (Figure 1). In the 3 recent cases of slow loris eating by adult female Yet and her female infant Yeni (Table 1), Yet seems to have diverted her travel path along her day route (ca. 40 m) to the location where the capture eventually took place, returning to the prior route after consumption (Figure 1). In each case, Yet turned abruptly (ca. 45°, Figure 1) towards the capture location about 5 min (i.e. 40m) before capture. After consumption of the loris she turned back sharply (i.e. ca. 90°, Figure 1), and made another 45° turn to continue her previous direction. There was no social event (i.e. the beginning or end of a party or a long call from a flanged male from a distance) at any of the three change-points in her route (i.e. prior to capture, after consumption, and continuation of her prior direction).

Capture started when the orangutan slapped the slow loris, which fell out of the tree, and finished on the ground when the orangutan caught the slow loris and killed it by biting the skull. The consumption process comprised the steps described by Utami and van Hooff (1997), that is, the female consumed the head, then the genitals, organs, limbs and other parts of the slow loris, however, in all 3 recent cases, the female ate the limbs immediately after the head. Data on total consumption time were available for the three recent cases of meat-eating (Tables 1 and 2).

Although meat sharing took place between the mother and infant, it occurred only when the mother was passively tolerant. Active giving by the mother did not occur. During the first recent case (February 2007), the infant made no attempt to eat the slow loris during the first 12 minutes after capture. Food sharing then occurred 11 times, including mouth-to-mouth feeding 3 times. Active resistance to food sharing by the mother occurred 3 times but only after 70 minutes of consumption. During the second case the infant made no attempt to eat from the slow loris during the first 20 minutes. During this case, hand-to-hand meat sharing occurred 34 times, mouth-to-mouth or mouth-to-hand occurred 5 times, and all 39 occurrences of food-sharing were initiated by the infant. Active resistance from the mother occurred 12 times during the first two hours of eating. No data on meat sharing...
are available for the third case (Table 1), but the infant ate part of the slow loris some minutes after her mother started to eat.

During the second case the mother had a mean bout duration (sec) of 27.1±SD 17.4, and a mean number of chews/bout of 24.5±SD 15.6 ($N_{bout}=22$, $N_{chews}=538$), the infant had a mean bout duration (sec) of 16.3±SD 16 and a mean number of chews/bout of 18.5±SD 13.4: ($N_{bout}=6$, $N_{chews}=98$). The mean chewing rate throughout consumption of the mother was 0.95±SD 0.25 chews/sec, with a maximum of 1.17 chews/sec, while that of the infant was 0.84±SD 0.29 chews/sec, with a maximum of 1.09 chews/sec. Chewing rate decreased with time for both the mother (Spearman’s Rho: $r=-0.625$, $N = 22$, $p = 0.002$) and the infant (Spearman’s Rho: $r=-0.899$, $N = 6$, $p = 0.015$). We were not able to determine the exact body parts being eaten at each moment and therefore it was difficult to assess how body part affected the chewing rates. The mean chewing rate for meat was lower than mean chewing rates for insects (1.32±SD 0.19 chews/sec, $N_{bout}=10$) and mature leaves (1.17±SD 0.02 chews/sec, $N_{bout}=8$) by the same mother (Kruskall Wallis: $\chi^2 = 20.108$, $df = 2$, $p < 0.001$; followed by a multiple comparisons post-hoc test: $p < 0.001$ between meat and insects, and meat and leaves).

After consumption of the carcass only a few pieces of bare skin remained, suggesting that the orangutans consumed all of their prey. The mother ate for 244 at 0.95 chew/sec, while the infant ate for 46 min at 0.84 chew/sec (i.e. the mother ate 1.13 times faster than her infant), meaning that they ate 85.7% and 14.3% of the total slow loris, respectively. Because all three cases concern the same type of meat eaten by the same individuals under the same social conditions (i.e. without any other individuals present), we assume that the chewing rates of the first and third case were similar to those of the second case. Using the mean chewing rate for the second case, the mother ate 63.3% and the infant ate 36.7% of the slow loris during the first case, and the mother ate 44.7% and the infant 55.3% during the third case. We assumed via visual assessment of the video recordings that the orangutan ate an adult male slow loris, which has a mass of 737 g (Nekaris & Bearder, 2007). Thus, across the three cases, this represents a maximum mean feeding rate of 160.9 g/h for an entire adult male slow loris by the adult orangutan and 142.4g/h by the infant (Table 2). If we assume that a slow loris has the same nutritional content as a squirrel, rabbit or red colobus monkey, 115kcal/100g (USDA Food Composition Database; Wrangham & Conklin-Brittain, 2003), then the adult female orangutan ingested 185 kcal/h and the infant ingested 163.8 kcal/h.
Table 2. Feeding time and rates on slow lorises by the focal mother and infant during the three recent cases.

| Year | Month    | Time (min) mother | Time (min) infant | Total time | Feeding rate mother (g/h) | Feeding rate infant (g/h) |
|------|----------|-------------------|------------------|------------|--------------------------|--------------------------|
| 2007 | February | 174               | 114              | 174        | 160.9                    | 142.4                    |
| 2007 | December | 244               | 46               | 244        | 155.3                    | 137.5                    |
| 2008 | April    | 140               | 196              | 196        | 141.2                    | 124.8                    |

Time (min) mother and time (min) infant = the time the adult orangutan female and her infant ate for. Total time = total observation time from moment of capture until end of consumption, during which mother and infant ate the slow loris either alone or together.

Ecological data

Five slow loris captures occurred in February and April and 1 in December (no dates were available for 3 cases; Table 1). The graphical representation of slow loris captures against (ripe) fruit availability (Figure 3a,b) suggests that orangutans may be eating slow lorises particularly during periods of low (ripe) fruit availability.

For Period A the observed mean fruit availability at the time of slow loris eating is (10.2% + 5.8%)/5 = 8.00%. The \( P_i \) of observing \( \leq 8.00 \) is 0.14. The observed mean ripe fruit availability at the time of slow loris eating is (1.9 + 3.6)/2 = 2.75 (\( P_i = 0.08 \)). For Period B, the observed mean fruit availability at the time of slow loris eating is (2.38 + 2.13 + 5.14)/3 = 3.22% (\( P_i = 0.11 \)) (Figure 2). The observed mean ripe fruit availability at the time of slow loris eating is (1.34 + 1.60 + 1.95)/3 = 1.63% (\( P_i = 0.23 \)). Combining the two periods, the \( P_i \) of observing a mean fruit availability of \( \leq 8.00 \) in period A and \( \leq 3.22 \) in period B is 0.016. The \( P_i \) of observing a mean ripe fruit availability of \( \leq 2.75 \) in period A and \( \leq 1.63 \) in period B is 0.017. These results show that slow loris eating by orangutans occurred significantly more often in periods of low fruit availability and low ripe fruit availability.
Figure 3a. Fruit availability 1991-1994, fruit range [5.6%-19.6%), ripe fruit range 1.9%-10.1%]. The slow loris symbol represents the date of slow loris captures by orangutans.
Figure 3b. Fruit availability 2006-2008, fruit range [1.8%-8.0%], ripe fruit range [0.7%-4.6%]. No data are available for April–August 2007 due to local political unrest. The slow loris symbol represents the date of slow loris captures by orangutans.
Discussion

Meat-eating in orangutans is a rare event, which makes it difficult to examine. Owing to the small sample size in this study, any generalizations should be treated with caution.

How do orangutans find slow lorises?

All known cases of slow loris capture and eating at Ketambe, including the 3 most recent observations, occurred at locations scattered through the area (Figure 1). Hence, encounter and predation of slow lorises by orangutans most likely occurred opportunistically, because the events were not related to any particular locations (Utami & Van Hooff, 1997). This is also often the case in other instances of predation by primates (see review in Stanford, 1998). Nevertheless, the 3 recent cases indicate that the adult female diverted her travel path to the location where the capture took place, returning to the previous route after consumption. Identifying potential travel goals is a major exercise in itself (Byrne et al., 2009). However, we tentatively interpret the orangutan’s deviation in her travel route in biological terms, suggesting that she had the goal of capturing a slow loris, for 3 reasons. First, if the turn was not the effect of a decision-making process, we would expect either straight-line or random travel. However, Yet turned abruptly (±45°, Figure 1) towards the capture location about 5 min (i.e. 40m) before the actual capture, suggesting that she did not anticipate a remembered site and travelled towards it in a straight line, nor was she traveling randomly and unexpectedly encountered a slow loris in her path. Moreover, Yet turned sharply back to her previous route after consumption, supporting the view that there was a meaningful cause for her previous deviation. Second, no social events coincided with the change points in her route. Third, the pattern in her travel route is consistent across the 3 recent cases (Figure 1) and does not coincide with the approach to other important food sources at Ketambe, such as fig trees (Wich, Hardus and Lameira pers. obs.). New methods (e.g. change-point test, Byrne et al., 2009) for objectively determining an animal’s travel path could be used to elucidate this matter in the future (e.g. Asensio et al., 2011).

Slow lorises are solitary nocturnal strepsirrhines, meaning that they are difficult to locate for a diurnal primate, such as orangutans (Bearder, 1987). Slow lorises live in the main canopy, prefer the forest edge (Johns, 1986) and sleep in sites like tree holes and crevices (Choudhury, 1992). If we accept that the orangutan changed her course towards the capture location purposely, then, although it is possible that the orangutan observed
the slow loris from a distance, she may also have been able to identify a potential sleeping location or micro-habitat (e.g. trees with particularly dense epiphytes). Alternatively, the orangutan could have used olfactory cues to find a slow loris. Lorises use olfactory communication (Charles-Dominique, 1977; Nekaris & Bearder, 2007) and a trained observer can smell a loris up to 50m away (Alterman (1995), thus, plausibly, slow loris olfactory communication may have also been intercepted by the orangutan. Future experiments should test this hypothesis.

**Meat sharing**

Similar to most primate species (Brown et al., 2004), meat sharing in orangutans occurred only between mother and infant, although in chimpanzees and bonobos it has also been observed between wild adult males and females (Rose, 1997; Stanford, 1999). No other adult orangutans were in the vicinity of our observed cases, so it remains to be determined whether the lack of meat sharing between adult orangutans is simply a consequence of semi-solitary living. Our results show that the infant initiated all meat sharing. This is similar to transfers of other foods between mother and infant orangutans (Jaeggi et al., 2008) and with food transfers in other mother-infant primates (Nishida & Turner, 1996; Rapaport & Ruiz-Miranda, 2002; Ueno & Matsuzawa, 2004).

**When and why does an orangutan eat meat?**

Because orangutans did not travel in parties while capturing a slow loris and did not share their meat with unrelated individuals, the ‘meat for sex’ hypothesis (Mitani & Watts, 2005; Stanford et al., 1994a; Teleki, 1973) and the male social bonding hypothesis (Mitani & Watts, 2001, 2005; Mitani et al., 2002; Takahata et al., 1984), are not applicable. However, we found that slow loris eating by an orangutan occurs significantly more often in periods of low fruit and low ripe fruit availability. Thus, the orangutan preyed on slow lorises during periods of food scarcity. We were unable to include data for the 1 case of slow loris eating in February 1992 in this test. However, this case occurred during a month with extremely low fruit availability and low ripe fruit availability, meaning that it is very likely that if including these data would strengthen our conclusion that slow loris eating occurs particularly in periods of low (ripe) fruit availability.

Several ecological factors and prey characteristics may affect seasonality of meat-eating in primates. Because orangutans and slow lorises both feed on fruits (slow lorises are...
only slightly less frugivorous than orangutans; Nekaris & Bearder, 2007), encounters followed by capture of lorises should increase in frequency when both species are attracted to common resources (Stanford, 1998). However, this is unlikely since orangutans are diurnal primates, whereas slow lorises are nocturnal and their sleeping sites are far from the nearest feeding site (K.A.I. Nekaris, pers. comm.).

Captures are also expected during the prey’s birth period (Boesch & Boesch-Achermann, 2000; Fedigan, 1990; Mitani & Watts, 2005; Rose, 1997, 2001; Takahata et al., 1984). However, orangutans have never been observed to eat young lorisines, making this explanation for the timing of slow loris capture improbable. Orangutans may simply capture slow lorises during food scarcity because they spend more time travelling in search of food, and thus, are more likely to encounter a slow loris by chance. This, however, is unlikely, since orangutans reduce travel and feeding time and increase resting time during food scarcity (Knott, 1998; Wartmann et al., 2010). Moreover, other differences in range may not be sufficient to explain the occurrence of slow loris hunting, because males have wider ranges than females (Singleton & van Schaik, 2001) but slow loris hunting is not biased towards males (van Schaik et al., 2009b), and because not all females of the same population, which experience the same periods of food scarcity, show this behavior.

Human observers are often oblivious to the presence of slow lorises in the forest and to the best of our knowledge they have not been observed during orangutan follows except when one is actually hunted by an orangutan. It is therefore difficult to provide a measure of encounter rate of slow lorises and to test whether orangutans target slow lorises during food scarcity. However, this may be assessed indirectly by examining an alternative hypothesis: that orangutans encounter slow lorises while foraging for dispersed food, such as insects, during food scarcity (van Schaik et al., 2009b). According to this hypothesis, time spent feeding on insects should be negatively correlated with fruit availability. However, we found no correlation between fruit availability and time spent feeding on insects by the female orangutan (Pearson correlation for 2007-2008: N = 11, r = -0.481, p = 0.134). Moreover, during the 2 periods (1991-1994 and 2007-2008), the maximum time spent feeding on insects recorded for this female was 25.8% (June 1993), but slow loris captures occurred when the female spent 12.9% (April 1993), 16.8% (February 2007), 16.7% (December 2007) and 7.4% (April 2008) of her time feeding on insects, indicating that this activity did not necessarily lead to more slow loris encounters. Further, when plotting time spent feeding on insects per month for all females living in the Ketambe
area, this particular female (Yet) did not seem to be an outlier compared to other adult females (Figure 4).

Evidence of orangutan meat-eating supports the fallback food hypothesis, contrary to findings for chimpanzees (Gilby & Wrangham, 2008; Gilby et al., 2006; but see Pusey et al., 2005; Stanford et al., 1994a). Marshall and Wrangham (2007) classify 2 fallback foods: staple and filler fallback foods. Staple fallback food serves as the sole food supply when preferred food is scarce and thus is an abundant food that is available year round. Filler fallback foods are rare and usually of high quality (Constantino & Wright, 2009; Marshall & Wrangham, 2007; Marshall et al., 2009b). Meat can be considered to be a filler fallback high-quality, energy-rich food for Sumatran orangutans, because the availability of preferred fruits is low when meat is eaten (Kaplan et al., 2000; Knott, 2005; Marshall & Wrangham, 2007; Marshall et al., 2009b; Milton, 1999). Although slow loris densities may be highly variable (Wiens & Zitzmann, 2003), they are nevertheless considerably less dense than other food sources usually considered as orangutan staple fallback foods (e.g. bark, leaves, figs), and they probably exist in densities more similar to those of other filler fallback foods, such as honey.

The saliva of the slow loris is toxic and is used in defense against predators (Alterman, 1995). Thus, orangutans should avoid such a risk when their dietary intake can be derived from available risk-free resources (e.g. ripe fruit). This risk might also explain why wild orangutans slap their slow loris prey out of the tree, to knock the prey unconscious and avoid being bitten, before descending rapidly to the ground to capture and kill the loris with a bite to the head. An unsuccessful attempt at capture on the ground (after slapping) at Suaq Balimbing, Sumatra (A. Permana, pers. comm.), suggests that orangutans may risk losing such a valuable prey to avoid being bitten.

Slow loris hunting likely represents a cultural behavior (van Schaik et al., 2003; Van Schaik et al., 2006) and this may explain why some individuals seem to be specialist slow loris hunters, but other individuals of the same population living in the same area do not show the behavior. Yet, whose capture rate is some thirty times higher than anyone else’s (van Schaik et al., 2009b), is the most dominant female in Ketambe, a status that may not favor social transmission of the behavior in semi-solitary orangutans. Future studies should focus on the family lineages of individuals showing the behavior, to address this question.
Chewing and feeding rates, and evolutionary aspects of meat-eating

The chewing rate of meat-eating in an adult orangutan was lower than when compared with insect and leaf chewing rates. This may be explained by the generally low fat percentage and collagen richness of wild tropical mammal meat, which makes it tough to chew (Lucas & Peters, 2000). Unpublished data for other cases of meat-eating by orangutans at Suaq Balimbing also show that individuals chew meat for several hours (C. P. van Schaik, pers. comm.).

Orangutans used more than twice the amount of time (160.9g/h) to eat the same amount of meat as the chimpanzee data used to support the cooking hypothesis (348g/h) (Wrangham & Conklin-Brittain, 2003; Wrangham, 2009). Other chimpanzee data shows that this species is able to consume meat at much higher rates (i.e. 1.9±1.2kg/h; Gilby, 2006). This difference between orangutans and chimpanzees may suggest that higher sociality in chimpanzees influences intake rates, where individuals are surrounded by conspecifics when eating meat, and where meat is a highly preferred food item and stealing occurs (Boesch & Boesch, 1989; Goodall, 1986; Stanford, 1999). In chimpanzees, feeding rates on meat are slower when there are many other individuals present (Gilby, 2006). Although this
seems to contradict the sociality hypothesis within species, the minimum values in these cases remains much higher than in orangutans (e.g. more than 500g/h with 10 beggars; Gilby, 2006), supporting the hypothesis.

One of the largest-brained australopithecines (i.e. *Australopithecus africanus*; McHenry, 1982) has an estimated energy requirement of 1202-1507kcal per day (Aiello & Key, 2002). According to orangutan data (ingestion rate of 185kcal/h), *A. africanus* would have had to chew for approximately 2h to achieve 25% of these caloric requirements purely from meat (Table 3, orangutans x A. africanus), while achieving the remaining 75% of its caloric requirements from food sources with faster chewing/intake rates (e.g. leaves or insects). This constitutes a considerable period of the day for orangutans, which spend approximately 6 hours a day feeding (Morrogh-Bernard et al., 2009), and does not include the time necessary for the collection of vertebrate prey.

In comparison with semi-solitary orangutans, australopithecines are assumed to have lived in social groups (e.g. Copeland et al., 2011). Therefore, an individual may not have been responsible for procuring all of its own calories, reducing search and hunt time. It is also reasonable to assume that biomechanics of the craniodental morphology between orangutans and chimpanzees do not sufficiently explain the differences in feeding rates on raw meat between both species. Therefore, group living as opposed to (semi-)solitary living may have played an important role as an intake accelerator. Higher sociality in australopithecines and *Homo* would have reduced the time needed to chew on meat by increasing feeding rates, as observed in chimpanzees (Table 3). Thus, time needed to chew on raw meat would not impede a social early human from consuming a 25% meat-based diet. These findings differ from the results of Wrangham and Conklin-Brittain (2003) in that we use a 25% meat diet in a human ancestor, instead of a 100% meat diet. We set the meat diet at 25% because excessive protein consumption is unhealthy for humans, becoming toxic or lethal when consumed too much by non-carnivores (Speth, 1987, 1989; Speth & Spielmann, 1983), and causing negative effects on babies (e.g. lower birth weights) when pregnant females surpass 25% protein in their diet (Speth, 1989, 1990). This implies that the cooking hypothesis (Wrangham & Conklin-Brittain, 2003; Wrangham, 2009), as a means to reduce time spent chewing on meat, will be further supported only when it is shown that meat represented more than a quarter of the total diet of our social ancestors.
Table 3. Time chewing on raw meat required to satisfy 25% of an individual’s energy daily requirements, compared with feeding rates of orangutans and chimpanzees and daily energy requirements of *Australopithecus africanus* and *Homo erectus*.

| Daily energy requirements | *Australopithecus africanus*: 1507 kcal/day<sup>a</sup> | *Homo erectus*: 2487 kcal/day<sup>b</sup> |
|---------------------------|-----------------------------------------------------|--------------------------------------|
| Feeding rate              |                                                     |                                      |
| Orangutans: 185 kcal/h    | 2.04h                                               | 3.36h                                |
| Chimpanzees: 400 kcal/h<sup>b</sup> | 0.94h                                              | 1.55h<sup>c</sup>                   |

<sup>a</sup>, Aiello and Key (2002); <sup>b</sup>, Wrangham and Conklin-Brittain (2003); <sup>c</sup>, c.f. Wrangham and Conklin-Brittain (2003).

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