Orangutan diet: lessons from and for the wild
Hardus, M.E.

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INTRODUCTION

Human activities such as logging, mining, poaching and land conversion for plantation development and other uses have had an enormous impact on biodiversity and the habitats of many different species of wildlife, and these activities and their impacts are still growing (Butchart et al., 2010; Hoffmann et al., 2011). Habitat and species loss are particularly pronounced in tropical rainforests, where biodiversity is high but the amount of natural habitat lost is also high (Miettinen et al., 2011; Myers et al., 2000; Sodhi et al., 2004). Protected Areas (PAs) are a potentially efficient way of protecting biodiversity (Bruner et al., 2001; DeFries et al., 2005; Gaveau et al., 2009a; Naughton-Treves et al., 2005), but their success is largely dependent on proper funding, community support, strong institutions, and law enforcement (Barrett et al., 2001). However, logging and poaching continue to occur inside protected areas, such as in Africa and southeast Asia wherein populations of endangered species occur (Meijaard & Wich, 2007). Moreover, these species may also live partly outside of PAs (e.g. Blanc et al., 2003; Meijaard & Wich, 2007; Morgan & Sanz, 2007; Rijksen & Meijaard, 1999), where destructive practices may occur with fewer restrictions than within them. Therefore, it is of paramount importance for biodiversity conservation to understand how species, especially large mammals, including great apes, react and potentially adapt to habitats with varying degrees of human disturbance (e.g. Campbell-Smith et al., 2011a; Meijaard et al., 2010a). To this end, conservation-oriented research is essential, as it provides information on species behavior and responses to anthropogenic factors. The outcomes of such research can then be used as input for practical guidelines for conservationists, politicians and other relevant stakeholders. Examples include guidelines for reduced logging impact on wildlife in general (Meijaard et al., 2005; Pokorny et al., 2005; Sist et al., 1998) and regarding taxonomic groups in particular, such as great apes (Ancrenaz et al., 2010; Hardus et al., 2012b; Morgan & Sanz, 2007; OCSP, 2010).

In addition to in-situ great ape conservation, reintroduction programs can also play an important role as maintaining sustainable numbers of individuals of endangered species in the wild (Beck et al., 2007; Russon, 2009). These programs release ex-captive animals, often rescued from the pet-trade, back into the species’ natural habitat. If the primary goal
of reintroduction is to establish self-sustaining populations in the wild or to re-establish extinct wild populations (Beck et al., 2007), the foremost concern is to assure individual survival of the released individuals. Successfully adjusting to forest life depends on a number of behavioral adaptations, related to food choices, nesting, and anti-predator responses (Rijksen, 1978). It is thus important to comprehend individuals’ natural behavior and predispositions in captivity, and how these may accelerate or delay adaptation to the new habitat into which they are being released, and consequently how these may affect survival chances in the short and long term. This is especially true with respect to the species’ diet because food constitutes the basis of all life activities, and food distribution and quality often shapes the organization of an animal’s social community.

Indonesia, the fourth most populous country on the planet, comprised of thousands of tropical islands, also boasts one of the highest levels of endemic species in the world, with over 646 species of mammals (i.e. more than 10% of the known mammalian species worldwide), 36 percent of which are endemic (Konsorsium Nasional Untuk Pelestarian Hutan dan Alam di Indonesia, 1995). Thirty of these species are primates, with unfortunately 22 of them being either endangered or critically endangered, largely as a result of human pressure on their ecosystems (IUCN, Red List 2011). One of these species, the orangutan, the only great ape found outside of the African continent is a major flagship species of Indonesia (i.e. charismatic species chosen to raise public awareness, action and funding; Leader-Williams & Dublin, 2000), is restricted today to the rainforests of the islands of Borneo and Sumatra. Orangutans are an umbrella species, meaning that these taxa have extensive habitat requirements, so that their protection also relates protection to a host of other species that share the same area (Ozaki et al., 2006; Roberge & Angelstam, 2004). In the case of orangutans, this implies that in undisturbed conditions, at least five other primate species, five hornbill species, 50 different fruit tree species and 15 liana species will also carry protection under the ‘umbrella’ of that covering the orangutan (Delgado & Van Schaik, 2000; Rijksen & Meijaard, 1999). However, as a result of deforestation and hunting (Meijaard et al., 2012), enhanced by the world’s most rapidly expanding equatorial crop (oil palm, Elaeis guineensis; Koh & Wilcove, 2008), the orangutan is one of the most threatened species of Indonesia, and the Sumatran orangutan (Pongo abelii) has been listed as one of the world’s 25 most endangered primate species (Mittermeier et al., 2008). Deforestation rates per year on the island of Sumatra are among the highest of the world (between 2000-2008/9: 0.9% in Aceh and 2.3% in North Sumatra; WWF-Indonesia, 2010), with Sumatran orangutans and other wildlife subsequently forced to live in disturbed forests (Rijksen & Meijaard, 1999; Singleton et al., 2004; Wich et al., 2011a; Wich et al., 2008). As a result the
species has been listed as critically endangered (Red List 2011), and without direct and committed intervention its habitat may largely disappear over the next few decades (Meijaard & Wich, 2007; Meijaard et al., 2012). The Bornean orangutan (Pongo pygmaeus) is listed as endangered by the IUCN (Red List 2011), however their conservation may rapidly become as urgent as for their Sumatran counterparts, particularly due to hunting pressure in combination with habitat loss in Borneo (Meijaard et al., 2011a; Meijaard et al., 2010b; Meijaard et al., 2012). As such, it is important for conservation research to identify the essentials of orangutan survival, and which human activities affect orangutans the most.

Food constitutes the fuel for all biological activities, such as body maintenance, growth, locomotion and reproduction. Deforestation directly affects food sources by damaging and altering forest structure and composition, thereby influencing the lives of forest inhabitants very rapidly. As such, feeding ecological research is a valuable tool for conservation. Thus, it is crucial to thoroughly comprehend what an orangutan’s diet consists of and how this diet is affected when individuals experience more or less drastic changes in their habitat (Soehartono et al., 2009).

Study species
Orangutans are semi-solitary and form temporal parties of variable composition (fission-fusion groups) loosely organized around a dominant male (Mackinnon, 1974; Mitra Setia et al., 2009). Orangutans may aggregate passively, such as during feeding, or actively, for instance when independent juveniles form travel bands (Sugardjito et al., 1987). These loose communities are suggested to move around seasonally in search of areas with abundant food (te Boekhorst et al., 1990). When large trees are fruiting, several orangutans can be seen feeding in the same tree, and at the Ketambe research site in Sumatra, a staple fallback food such as large strangler figs (Ficus sp.) can attract up to 15 individuals in and around one single feeding tree (Utami et al., 1997). Wild orangutans are mainly frugivorous, but also feed on leaves, flowers, bark, and insects, and they also been seen to consume mammal meat (Hardus et al., 2012a; Morrogh-Bernard et al., 2009; Russon et al., 2009; Utami & Van Hooff, 1997). Sumatran orangutans at Ketambe have been observed to feed on a total number of 512 plant items from 379 different plant species (Russon et al., 2009). Individual diets contain at least 100 different plant species, but likely many more as after more than 2,800 follow hours per orangutan (Augustus 2003-June 2009; M.E. Hardus unpublished data), individuals are still observed to consume additional plant species for the first time.
In Sumatra, orangutan reintroduction programs began to release ex-captive orangutans into the wild during the 1970’s (Frey, 1978; Rijksen, 1978), but the success of such reintroduction work is virtually unknown (Zweifel, 2009), although it has been documented that some individuals have successfully reproduced in the wild (cf. Trayford et al., 2010). Reintroduced orangutans are confiscated either from the pet trade or from forest fragments and many of them have spend relatively long periods of time in households. After confiscation, orangutans are rehabilitated in centers before they are released back into the wild. Because IUCN guidelines on great ape reintroduction stipulate that ex-captive, rehabilitant orangutans should not be released into areas where resident wild populations occur (Beck et al., 2007), release sites are likely to differ in ecology from their place of origin. Knowledge about which food items can be eaten and which should be avoided is crucial for survival, and is of particular importance to know in terms of increasing the chances of reintroduction success (e.g. Beck et al., 1991; Russon, 2009; Vogel et al., 2002). In golden lion tamarins (Leontopithecus rosalia), for example, consumption of toxic fruits and starvation caused the death of nearly 20% of the reintroduced animals (Beck et al., 1991), and an inadequate diet is one of the common causes of death for reintroduced orangutans (Russon, 2009). This reinforces the importance of comprehending how orangutans learn which items to include in their diet, food preferences and correlates, so that survival of individuals in reintroduction programs can be better maximized.

Aims and overview of the thesis

In this thesis, I examine several aspects and determinants of orangutan diet at individual and species levels. Up to now, most orangutan studies on diet have focused on broad diet categories at the population level. As such, this study presents results at a new level of detail, which is a necessary step to better understand orangutan behavior and predict how (reintroduced) orangutans can survive and adapt to habitat changes (and to their release in unfamiliar forest). I started this study in 2007 on the island of Sumatra, with this thesis containing the main findings of 2.5 years of field and experimental work.

In chapter 2, I study the effects of logging on the individual behavior of orangutans. The chapter focuses on the changes in forest structure brought about by logging, and how orangutan behavior differs between a pristine section of forest as compared to a selectively logged section of the same forest. The research area of Ketambe, Sumatra, Indonesia (part of the Gunung Leuser National Park and Leuser Ecosystem), has been partially subjected to intense but selective logging during the years 1999-2002. Whilst condemnable, this provides a unique opportunity to address the important question of the impact of logging on
individual orangutan behavior. I specifically focus on orangutan food resources, their activity budget, dietary composition, height of activity in the vegetation and locomotion. Based on the results, recommendations are given for conservation research, as well as guidelines for reduced-impact logging.

In chapter 3, I focus on the diet composition of 8 wild orangutans at Ketambe in order to make a further assessment of the logging impact in this population (chapter 2). At the same time, in this chapter I examine whether diet overlaps between individual, adult parous females, using data that were collected over a period of 7 years. Dietary overlap of individual orangutans was examined at the level of fruit and figs species by testing the effects of food availability at the plant species level, association time (i.e. the time orangutans were in association with each other for example when feeding or resting) and/or overlap in home range on diet similarity between individuals.

In chapter 4, I further investigate a specific aspect of the diet of a particular female of the Ketambe population, namely the capture and the subsequent consumption of mammal meat. This behavior has seldom been observed during the several decades of research conducted at Ketambe. I use all data available on such incidences to investigate how, when, and why an orangutan consumes meat. Furthermore, I use data on orangutan chewing rates on raw meat as a model to calculate the time necessary for early hominins to consume meat without the aid of cooking. Moreover, I compare data on raw meat consumption in orangutans and chimpanzees and offer some insight on the factors affecting raw meat consumption in the human lineage. This chapter reemphasizes the importance of collecting data at the individual level. Moreover, it shows how rare natural behaviors, which may easily be disrupted by human disturbances (van Schaik, 2002), can provide insights into other disciplines.

In chapter 5, I examine the acceptance and consumption of novel and familiar foods by individual captive orangutans. I perform experiments to understand how orangutans (Pongo pygmaeus, P. abelii, and their interspecific hybrids) react towards novel food, and how their reaction is influenced by gender, birth location and species. This is especially important for 1) conservation efforts, where wild orangutans live in degraded habitats with novel food (plants that colonized the disturbed area, or in the form of plantations), and for 2) reintroduction programs, where released orangutans need to incorporate novel food into their (rather restricted) diet repertoire. This experimental study was carried out in three captive orangutan groups, at Great Ape Trust of Iowa (US), Apenheul Zoo (The Netherlands) and BatuMbelin Quarantine Center (Indonesia).
In chapter 6, I present an experimental study conducted with the same three captive groups, which builds upon the results of chapter 5. Specifically, it poses the question, how may rehabilitant orangutans increase their acceptance and consumption of novel food to increase dietary diversity? The experiments in this chapter test the effects of both repeated exposures and sociality on the acceptance and consumption of novel food. In addition to chapter 2, this chapter provides further guidelines for reintroduction projects.