Small scale human-primate behavioural interactions in Amazonian Ecuador

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Declaration of originality

This dissertation is my own work and contains nothing which is the outcome of the work of others or in collaboration with others, except where indicated below.

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ABSTRACT

The investigation of predator-prey interactions has a long history in ecology, but most studies have focused on the lethal effects of non-human predators. Population declines of prey species because of human hunting are well documented, and much effort has been dedicated to quantify hunting sustainability. However, non-lethal effects of human hunting may also impact hunted species. This thesis aims to integrate methodologies from various disciplines to study the behaviour of Waorani hunters in Amazonian Ecuador, and the behaviour of one of their primary prey groups, primates.

In conservation biology, various assumptions are made about hunter spatial behaviour, such as the use of uniform circular areas around communities for resource extraction. This research demonstrates that these assumptions are not valid in the study system, and develops an alternate method for determining hunting pressure. Methods from animal behaviour are used to describe the spatial distribution of hunters and non-hunters. Interviews are also used to investigate perceptions of prey animals by the Waorani, with a particular focus on the role of primates. Primate behaviour is investigated in the context of non-lethal effects of human hunting. Changes in short and long term behavioural patterns are demonstrated using experiments with Poeppigi's woolly monkeys (*Lagothrix poeppigii*) and observations of red titi monkeys (*Callicebus discolor*). Key differences in behaviour were found between groups with and without recent exposure to human hunters. These differences suggest human hunting of primates has additional non-lethal effects which should be considered when assessing hunting sustainability.

Behaviour is recognised as an important component of human-environment interactions, yet the behaviour of humans and the animals they interact with is often overlooked. This thesis investigates behavioural interactions by focusing on individuals and groups on a small geographic and temporal scale, quantifying these interactions in the context of human hunting, and considering their implications for conservation.

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Chapter 1

Introduction

1.1. Humans and the natural environment

Humans are dominant organisms worldwide and have spread to most habitats outside the polar circles. Hannah et al. (1994) estimated that just 52% of the world's surface is undisturbed by human impact, but this percentage has significantly decreased to less than 25% in a more recent estimation (Ellis and Ramankutty 2008). This decrease is partly due to different methodologies, but also an increased understanding of the way in which humans impact the natural environment. The original estimate in 1994 measured almost the entire Amazon basin as undisturbed, when in fact human hunting and resource use occurs even in areas which are not deforested, and these activities can have a significant impact on ecosystems. Other research has demonstrated that human landscape modification, such as controlled burning of large areas, has a long history worldwide (Hayashida 2005). Although the prevalent ideology in conservation is one of humans as a source of unnatural disturbance (e.g. Young et al., 2005), rather than an integral part of the natural environment, the existence of extensive anthropogenic biomes is testament to the worldwide integration of humans in the natural environment (Ellis and Ramankutty 2008).

Although western philosophy sets humans apart in a dichotomy with nature, humans are just another component of the ecosystem, albeit with complex and unique behaviours (Goudie 2006). Like all species, they modify their environment, whether intentionally or unintentionally. Just as animals disperse the seeds of fruits they consume (Stevenson et al. 2002), so do humans (Rival 2002). Large herbivores can change the ecological conditions of their environment through soil enrichment (Feeley and Terborgh 2005) or overgrazing, and humans remove plants for firewood, construction and consumption (Kusters and Belcher 2004). In spite of these parallels, integrated approaches to biology which view humans as part of an ecosystem, rather than a potentially destructive outside force, are relatively novel (Berkes 2004). The work described in the following chapters aims to take an integrated approach to examining human interactions with the environment, focusing on predator-prey relationships and associated behaviour. Although hunting is only one of many anthropogenic factors that could affect biodiversity conservation, it offers an excellent opportunity to study local scale interactions between humans and their environment. In particular, this thesis aims to study these interactions from both the perspective of the predator and prey, using interdisciplinary methodologies.

The recent appreciation of the importance of behaviour for conservation can be demonstrated both by the birth of a new discipline, conservation behaviour, and the increase of behaviour-focused research in conservation journals (Buchholz 2007). Understanding the behaviour of human hunters and their prey can increase our understanding of hunting sustainability (Fitzgibbon 1998). For example, heterogeneous land use by human hunters may explain why hunting which occurs at locally unsustainable levels does not result in prey species population crashes (Salas and Kim 2002). Nevertheless, an investigation into the behavioural interactions between human hunters and their animal prey has not been fully realised – the behaviour of hunters and prey species is generally believed to be static in time and space, contributing little to the overall sustainability of wildmeat extraction (Van Vliet et al. 2010). These assumptions are not made in current theory on animal predator-prey interactions, which recognises the role of changing behaviour in predator-prey dynamics.

Changes in predator and prey behaviour occur over time, as prey develop behavioural adaptations to avoid predators, and predators change their behaviour to catch the prey (Boesch 1994). Gil-da-Costa (2007) noted the predatory behaviour of two radio-collared harpy eagles (*Harpia harpyja*) that were re-introduced to an island, and anti-predator responses given by naïve howler monkeys (*Alouatta palliata*). They found that the harpy eagles began hunting by perching close to monkey groups and giving a distinct call, which the researchers have named a “predator-assessment” call. In 35 observed cases, when the monkeys responded chaotically or showed little vigilance after the call, the eagle was more likely to attack or approach. However, if the monkeys were vigilant, the eagle delayed their attack or moved on to a different group. Over time, the howler monkeys developed an appropriate anti-predator response to harpy eagle predation (Gil-da-Costa et al. 2003). Although human hunters also encounter naive prey as they move into new areas, and some of these species are likely to adapt behaviourally to the new predator, this type of interaction is rarely recognised in the literature on human hunting. Likewise, reviews of animal anti-predator behaviour often do not discuss humans as potential predators, even if they recognise the extent of human predation (e.g. Ferrari 2009).

1.2. The effect of hunting on primate[1] behaviour

Although humans are the main predator of primates in some areas (Urbani 2005), little work has been done on primate anti-predator reactions to humans. Zuberbühler (2006) argues that high levels of human offtake are evolutionarily recent, so primates have no evolved response. However, humans have been hunting at high levels for long periods, including historically hunting some primates to extinction, such as in Madagascar (Godfrey and Irwin 2007). Furthermore, humans have been present throughout primate ranges for thousands of years, and in the case of African primates, hundreds of thousands of years (Goudie 2006). Although primates may have no evolved anti-predator response to humans, it is unlikely they have no anti-predation strategy, particularly given the rapidity with which primates have been shown to develop strategies for other predators (Gil-da-Costa et al. 2003).

The primate literature states that the freeze response is the most frequent response to humans; as human hunters can pursue any encountered prey, remaining inconspicuous may be the best strategy. However, little empirical evidence of this observation has been offered. Diana monkeys (*Cercopithecus diana*) do not react consistently to human hunters, with groups showing fight, flight and freeze reactions (Zuberbühler et al. 1997; Zuberbühler 2000), and work on putty-nosed monkeys (*Cercopithecus nictitans*) suggest a similar result (Arnold et al. 2008). Anti-predator responses to humans may vary with other species characteristics. For example, species which spend more time resting, and relatively little time feeding are likely to be less impacted by freezing in response to humans than those which need to feed frequently in order to acquire enough nutrition. The impact of freezing as an anti-predator response on species fitness may also depend on how often humans are encountered and how long the human remains close. Reactions to humans may also depend on the behaviour of the human encountered. Gil-da-Costa et al. (2003) showed that howler monkeys learnt appropriate responses to eagles. Primates may learn to use behavioural cues of predators and only respond to individuals which are actively hunting.

Anti-predator responses to humans can be hard to assess, particularly as researcher presence can alter the behaviour of study animals. The above studies focused on short term effects of human as predators, and their implications for primate cognition, but other studies on primate behaviour have assessed long term effects of human predation on other primate needs, such as food and social

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[1] Although humans are primates, primate is used to refer to non-human primates throughout this thesis. This use of the word primate, excluding humans, is not intended as an indication that humans are considered apart from all other organisms, but rather an editorial note to increase the readability of this thesis.

behaviour. These long-term effects are behavioural changes which occur even the in the physical absence of predators. Studies of long term effects of human hunting on primates have found decreases in calling and increased use of higher tree strata in areas with higher hunting (Watanabe 1981; Koné 2004). However, these investigations have been conducted on habituated and semi-habituated groups. The conclusions of these studies should be carefully considered, as the habituation process is likely to have changed the perceived risk of humans for these groups. It is not possible to know how researcher presence changes anti-predator behaviour, even in unhunted areas. Predators, and particularly human hunters, may be less likely to attack groups accompanied by a human, but human presence in the form of a researcher may increase stress and vigilance even in habituated groups (Klailova et al. 2010).

1.3. The landscape of fear

Studies of long-term effects of predators often recognise spatial heterogeneity in predation pressure, and compare spatially separated groups which are more or less exposed to predators (e.g. Watanabe 1981; Koné 2004). These differing predation pressures can be represented using the landscape of fear, which was proposed in 2001. The theory of the landscape of fear has been rapidly adopted in the ecological community, due to its accuracy in predicting prey behaviour and its applications for the integration of predator and prey spatial distribution (Laundré et al. 2010). The landscape of fear is a three-dimensional space, two of which are the geographical coordinates of an area, and the third dimension is a variable measure of fear, or perceived predation risk. The landscape of fear could have many applications in conservation, such as predicting spatial distributions of human prey species. Although some research has investigated the potential impact of human hunting on the distribution of species which are recreationally hunted (e.g. Tolon et al. 2009), no research has yet been conducted on humans as predators in the landscape of fear. This may in part be due to the divergent methodologies used to describe human and animal space use. Whilst the majority of animal behaviour studies rely on GPS trackers attached to individual animals, models of human wildmeat hunters have not yet adopted the more complex and accurate methodologies currently used to analyse animal movement (for example Willems & Hill, 2009).

Although research on human hunters recognises the importance of spatial heterogeneity (Van Vliet et al. 2010), models which simulate hunting pressure usually assume a section of the landscape receives uniform hunting pressure (Salas and Kim 2002), or that hunting pressure gradually decreases as distance from a community increases (Levi et al. 2009). Spatial variability in use is often investigated by zoning large blocks of land, either by the researcher or communities (e.g. Sirén et al. 2004), or by some characteristic of the land itself (for example, primary and secondary forest, as studied by Parry et al. 2009). Although these methods are rapid and such zones can be ecologically and culturally valid, categorical zones may fail to capture differences in the landscape at different spatial or temporal scales (Conner et al. 2003). Furthermore, these zoning methods do not result in an axis of variable predation risk, which could be used to describe the landscape of fear. Landscape ecology is a growing field which has developed many data-collection and analysis methods for describing the movement and spatial location of animals, and can be adapted to investigate human hunting in a manner which is compatible with studies on the landscape of fear.

1.4. Integrating disciplines in conservation

Many papers have discussed the importance of interdisciplinary studies in conservation, particularly integrating humans and social sciences into research (e.g. Caro 1998; Drew and Henne 2006; Milner-Gulland and Rowcliffe 2007; Shackeroff and Campbell 2007). However, integrating disciplines is not so straight-forward, and there are many obstacles to overcome. The theory and underlying values of different disciplines, difficulties in communication due to divergent discourse features and terminology, and difficulties in remaining up to date in diverse fields have all between identified as sources of potential conflict in interdisciplinary studies (Campbell 2005; Drew and Henne 2006; Fox et al. 2006).

When considering the sub-discipline of conservation behaviour, one of the primary obstacles to interdisciplinary studies which include humans lies in methodological differences between studies of human and non-human behaviour. Ease of communication between the researcher and human subjects has lead to a wide variety of research methods which are simply not possible with non-human subjects. Whilst studies of animal behaviour rely on observation and carefully designed experiments, studies of human behaviour can also use methodologies which rely on complex communication between the researcher and subject. These emic approaches, which attempt to view behaviour from the perspective of the actor, have many advantages and are widely used in the social sciences (Drew and Henne 2006). However, these differences can create issues when attempting to integrate or compare studies of animal and human behaviour. An example of the differences in approach can be seen in the above paragraph describing heterogeneity in human hunting. Studies of spatial heterogeneity in animal predators and prey relies on GPS and complex analyses, whereas studies of spatial heterogeneity in humans most often relies on interviews, drawn maps or guided trips through hunting territories. When integrating data collected using two different methodologies, differences in bias, temporal and spatial scales and precision may mean data are not directly comparable. In contrast, for example, using GPS trackers on human hunters could be combined with GPS tracked animal predators and prey species to develop a landscape of fear and investigate the impact of human hunting on spatial and temporal landscape use of non-human animals.

Closing this methodological gap could also simulate the exchange of theory and ideas across disciplinary boundaries, further developing conservation theory and practice. As it is not possible to communicate with most animal subjects, closing this methodological gap depends on adoption of methods from animal behaviour studies to investigate human behaviour. This call to adopt methods from animal behaviour studies should not be viewed as a call to abandon methods more traditionally used to study human behaviour, but rather an opportunity to complement current methods and increase the applications of human behaviour studies for conservation.

1.5. Thesis objectives

In this thesis I will investigate hunter-prey interactions in a single case study system. I explore the significance of primates to those who consume them, develop novel methods to describe spatial aspects of human hunting behaviour and investigate the effect of human hunting on the behaviour of unhabituated primates. Specific objectives are to:

1) Investigate how human hunters and those who consume primates perceive their prey.

2) Examine changes in human forest behaviour dependent on the purpose of a forest visit.

3) Investigate whether prey species use human behaviour to assess the relative threat level of different humans.

4) Describe the long term effects of human hunting on the behaviour of unhabituated primates.

1.6. Thesis structure

Chapter two describes the study area, and the culture of the Waorani people who participated in this investigation.

Chapter three places primates in Waorani culture. This thesis focuses on primates as human prey, as they are known to be important contributors to Waorani diet, but it is unknown how the Waorani themselves view primates. I argue that examining the place of a studied species in the ethnobiology of a culture is an important first step for any project.

Chapter four uses methods normally used to describe animal behaviour to quantify Waorani hunting behaviour. The technology used by Waorani hunters, and the prey they hunt, has previously been described, and is very similar to most lowland Neotropical hunting societies. This chapter however describes human hunting in a way which is comparable to descriptions of the behaviour of animal predators, and quantifies differences in forest use between hunters and gatherers, to demonstrate the benefits of adopting methodologies from movement ecology.

Chapter five focuses on the most heavily hunted primate in the area, Poeppig's woolly monkey (*Lagothrix poeppigii*). I use experiments to investigate the short-term effects of hunters and other humans on woolly monkey behaviour. Specifically, I investigate whether differing reactions to more and less threatening humans could explain the variability in anti-predator responses to humans in other primate species.

Chapter six investigates the long term effect of hunting on the behaviour and density of a less hunted species, the red titi monkey (*Callicebus discolour*). I use playbacks of red titi monkey loud calls to compare the density of the species at two sites, and determine the impact of hunting on spontaneous morning choruses of these loud calls.

The final chapter synthesizes the results of the entire thesis and discusses the implications of this research for conservation and primatology.

Additional information on current Waorani hunting methods are included in Appendix 1.

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Chapter 2

Study Site

2.1 Ecuador and the Amazon

Research was conducted in Yasuní National Park, the largest protected area in Ecuador's Amazon region. Ecuador, a small country located on the equator and the Pacific coast of South America, is split into four main cultural and ecoregions; Amazon, Andean Highlands, Coast and the Galapagos Islands. The Amazon region in Ecuador is split into 6 provinces which cover a total of 120,000km^2, and is located on the far west of the Amazon (Figure 2.1). Approximately 740,000 people live in these provinces (Ecuadorian Census, 2010), mostly members of indigenous tribes and immigrant groups from other regions in Ecuador. The Amazon also holds vast oil reserves which are exploited by various companies, and oil is Ecuador's main export. The area has also been described as having the highest biodiversity in South America (Bass et al. 2010).

2.2 Geography and Climate

The Ecuadorian Amazon is part of the core Amazon – a region with particularly high annual rainfall and no pronounced dry season (Bass et al. 2010). Throughout the year, sunrise and sunset occur at approximately 6am and 6pm respectively. Average daily temperature ranges between 20 and 35°C (Figure 2.2), and humidity is over 60% throughout the year (Figure 2.3). Yasuní National Park covers 9,820km^2 between the Napo and Curaray Rivers, and extends to the Peruvian border. The adjacent Waorani Ethnic Reserve covers approximately 6,000km^2. Both the Park and Reserve have low human population densities, and are mostly occupied by Waorani and Quichua peoples. In Yasuní National Park, the land is approximately 200-300m above sea level, and two main types of Amazonian forest are observed: vareza, which is seasonally flooded forest, usually along the banks of rivers, and terra firme, higher land which

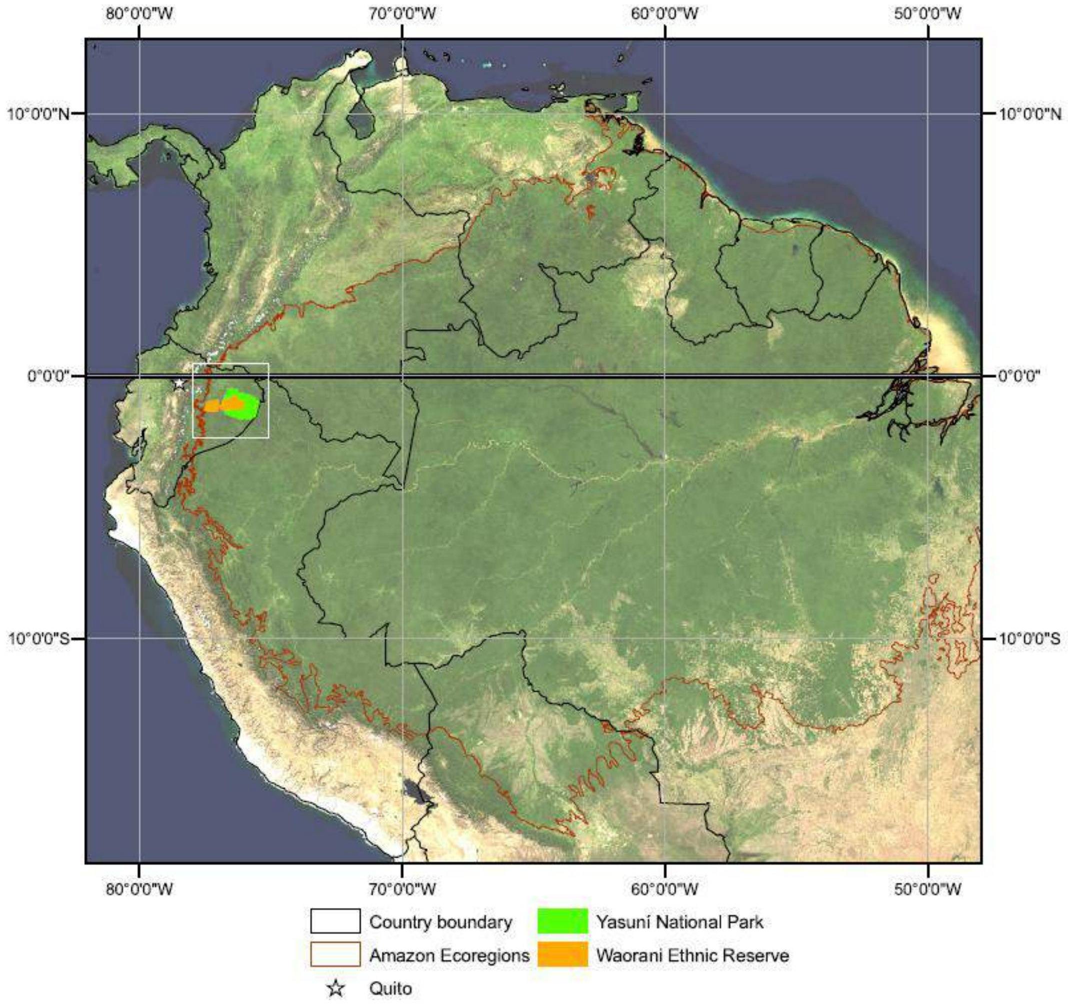

Figure 2.1. The location of Yasuní National Park and Waorani Ethnic Reserve in Ecuador and the Amazon ecoregion. Map from Finer et al. (2009).

occurs in the interfluvial areas (Valencia et al. 2004). Rivers are generally meandering, and oxbow lakes are common.

2.3 Threats to biodiversity and human rights

With almost 600 bird species, high amphibian, reptile and mammal diversity, and the highest measured tree diversity anywhere in the world, Yasuní National Park deserves its designation as a UNESCO Man and Biosphere Reserve (Bass et al. 2010). There are numerous long term research programmes inside the park, which have documented the biodiversity of the area. However, this high biodiversity also faces many threats, which include the presence of oil extraction facilities (Suárez et al. 2009) which have been exploited since the 1940s (Finer et al. 2008) and hunting by indigenous communities (Suárez et al. 2009). Logging in the south of the park – which had implications both for the biodiversity of the area, and also the human rights of some tribes who live in voluntary isolation within the park – has reportedly been stopped by increased monitoring of access roads (Finer et al. 2009). In spite of these threats, and particularly when compared with the extensive deforestation occurring in other parts of the Amazon, Yasuní National Park is relatively pristine (Bass et al. 2010).

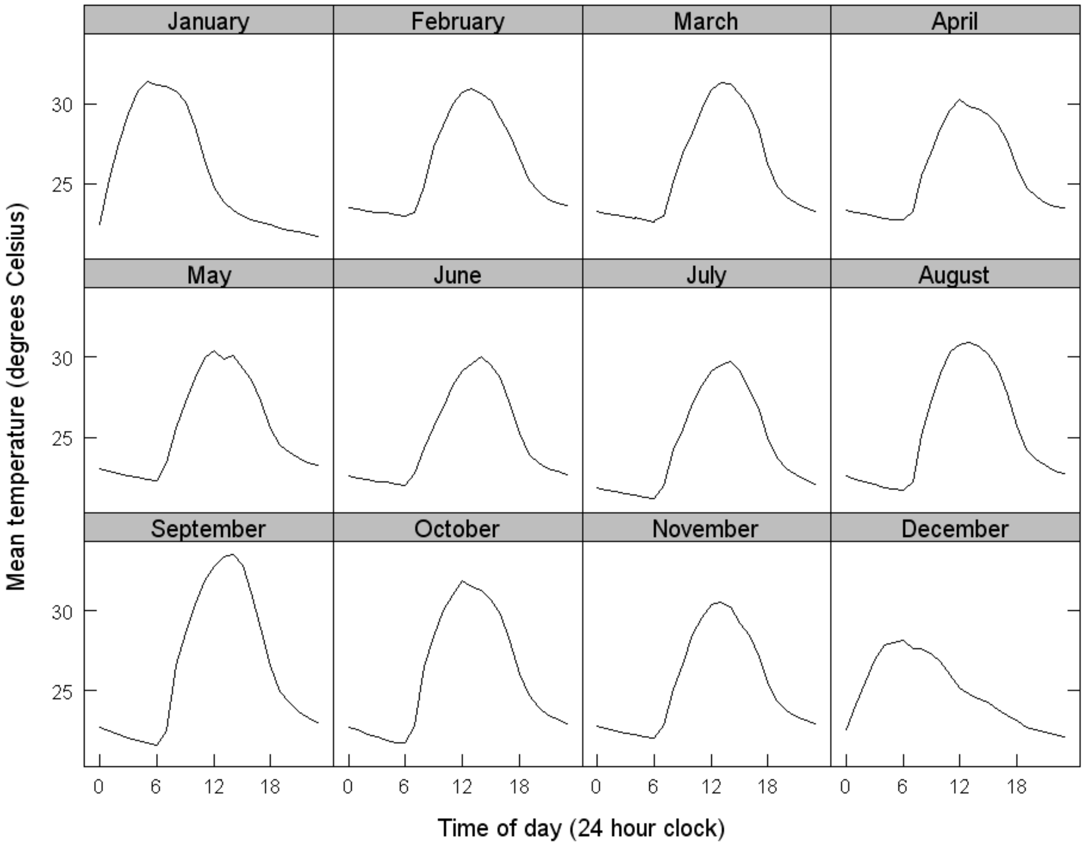

Figure 2.2. Mean daily temperature variation by month in Yasuní National Park from February 2010 to January 2011. Data collected by the weather station at Yasuní Research Station, available online from (http://www.yasuni.ec/dcyasuni.php?c=1253).

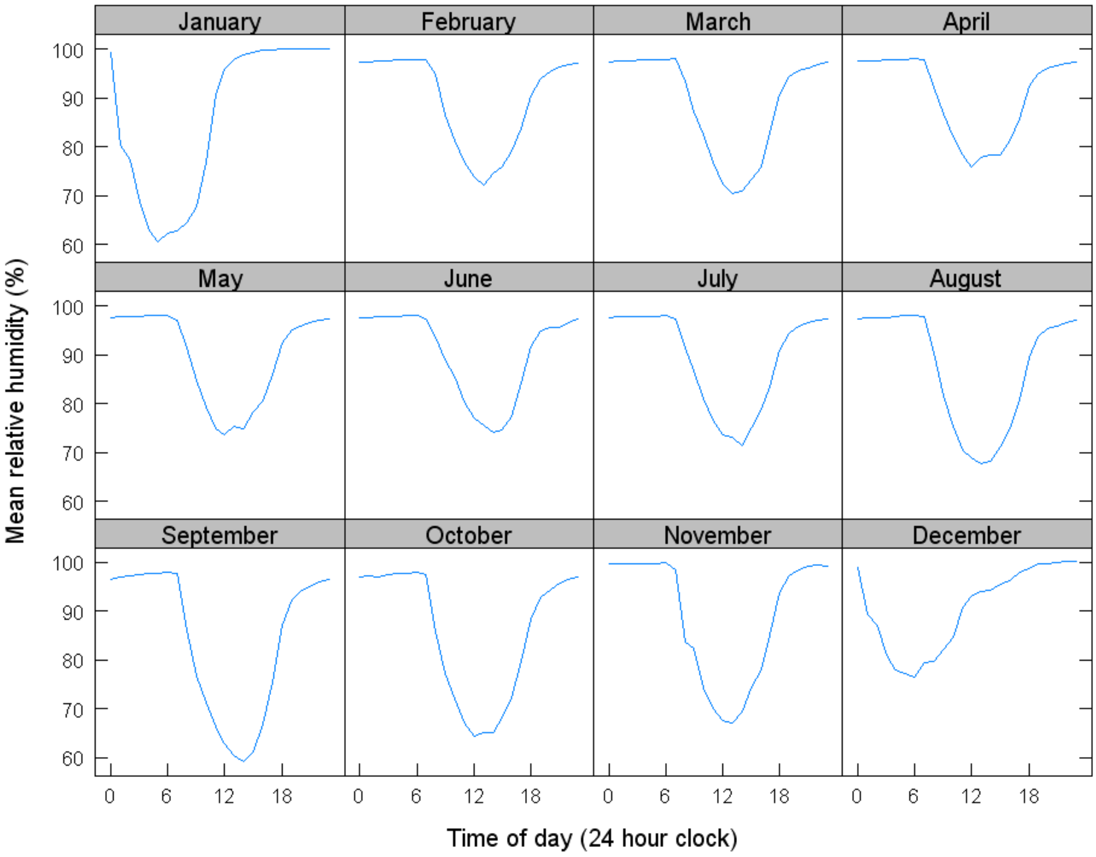

Figure 2.3. Variation in mean daily relative humidity by month in Yasuní National Park from February 2010 to January 2011. Data collected by the weather station at Yasuní Research Station, available online from (http://www.yasuni.ec/dcyasuni.php?c=1253).

2.4. Primate species in the area.

Twelve primate species are present in Yasuní National Park, although just 10 are present in the study area (Table 2.1). Biological research is conducted throughout Yasuní National Park, but research has primarily been conducted near the two research stations in the north of the park which are used in this study; Tiputini Biodiversity Station (TBS) and Yasuní Research Station (YRS). All primate species in the park have experienced some degree of research, as a result of several long term projects headed by Antony Di Fiore of the University of Texas at Austin.

Table 2.1. Primate species observed at TBS and YRS, Yasuní National Park.

Common name	Scientific name
White-bellied spider monkey	*Ateles belzebuth belzebuth*
Poeppigi's woolly monkey	*Lagothrix poeppigii*
Red howler monkey	*Alouatta seniculus seniculus*
White fronted capuchin monkey	*Cebus albifrons aequatorialis*
Common squirrel monkey	*Saimiri sciureus macrodon*
Noisy night monkey	*Aotus vociferans*
Red titi monkey	*Callicebus discolour*
Equatorial saki monkey	*Pithecia aequatorialis*
Pygmy marmoset	*Cebuella pygmaea*
Golden-mantled tamarin	*Saguinus tripartitus*

2.5. Focal primate species

2.5.1 Woolly monkeys (*Lagothrix poeppigii*)

Woolly monkeys are diurnal primates which live in large, overlapping social groups. These multi-male, multi-female groups occupy large, overlapping home ranges of around 100 to 130 hectares. Groups are very tolerant of neighbouring groups, with whom they sometimes combine to form supergroups. Although staying close at night, social groups spread over large areas during the day for feeding (Di Fiore 2003). They feed mainly on fruits, favouring *Inga* and *Ficus*, with animal prey forming the second largest aspect of their diet (Di Fiore 2004). At TBS, a number of individuals have been radio collared, and the social groups of these individuals have received varying levels of habituation since 2005 (Di Fiore et al. 2009).

Woolly monkeys are reported to be a preferred prey of human hunters in the Amazon, partially due to their relatively large body size (mean weight of hunted individuals is 6.1kg at the study site, Franzen, 2006), and their desirability as pets (Peres 1991). At the study site, woolly monkeys are estimated to be killed at a rate of over 200 per year (derived from Franzen, 2006). They can live up to 30 years (Morand and Ricklefs 2005), and have high population densities compared with other primate species (Derby 2008), but like all primates have low intrinsic rates of reproduction, which contributes to their extirpation in areas where hunting pressure is great. Even though harpy eagles and jaguars prey on similar-sized howler monkeys (Peres 1990; Peetz et al. 1992), there is only one published record of a non-human predation on woolly monkeys (Ferrari 2009), and human hunters are likely to be their most significant predator, particularly in the specific study area.

2.5.2 Red titi monkeys (*Callicebus discolor*)

Titi monkeys are small, diurnal primates which live in groups consisting of pair-bonded adults and their sub-adult offspring. The taxonomy of the genus *Callicebus* has been revised many times, from two species in 1963, to 28 species in 2002 (Roosmalen et al. 2002). This latest revision designates the species present in the study area as *Callicebus discolour*. The male and female of each group perform regular duets, believed to function for group spacing (Oliveira and Ades 2004), but may also function as territory or mate defence. Previous research on the titi monkeys in Yasuní National Park found they spend approximately 42 per cent of the time feeding, and 15 per cent of time engaging in social behaviours. Fruit made up 63% of the diet, mostly from the families Cecropiaceae, Fabaceae and Melastomataceae, though they also eat leaves, flowers and wood (Carrillo-Bilbao et al. 2005). At TBS, there are a number of radio-tagged and habituated groups, which are part of long-term field research (de Luna et al. 2010)

Titi monkeys caught by human hunters at the study site weigh approximately 0.7kg (Franzen, 2006). Although hunted, they are not a preferred species and are extracted at low rates, particularly when compared with larger bodied primates. Yet due to the social structure of titi monkeys, even a low hunting rate could have a profound effect on population density. Both male and female contribute to infant-rearing, with the female providing milk and the male carrying infants (Fernández-Duque et al. in press). If one adult in the group is killed, the survival of dependant offspring will be low, and in order to successfully reproduce again, the widowed adult will need to find another mate. Observations of *Callicebus moloch* in captivity suggest that a female titi will not give birth for around a year after pairing with a new male, even though gestation period is approximately 128 days (Valeggia et al. 1999). In the wild, a variety of non-human predators, such as raptors, also attack red titi monkeys (de Luna et al., 2010)

2.6 Social history of the region

At the time of the first European exploration of the Amazonian area of Ecuador, diverse cultures were recorded trading along the River Napo to the Andean foothills. These cultures were mostly reliant on agriculture, and supported large population centres. More powerful groups captured and traded slaves from neighbouring groups. However little is recorded about these smaller groups from which slaves were taken, particularly those located away from the main rivers (Cabodevilla 1994). After the Spanish conquest in the 16th Century, the human geography of the area changed markedly, as many cultures were hit hard by European diseases for which they had no resistance; Andean groups started to migrate to the Amazon; and European settlers fought to have indigenous people to work on their farms or live at their mission posts (Rival 2002). Many cultures recorded by the first explorers are now extinct, and some present-day indigenous tribes of Ecuador are believed to be mixed-culture refugees of this period, who formed alliances and combined cultures (Cabodevilla 1994). Although some people lived on the larger rivers in the area, it is believed that the Waorani people have occupied the interfluvial areas between the Napo and Curaray Rivers (approximately the area of the present day Yasuní National Park and Waorani Ethnic Reserve) since at least the late 1800s (Finer et al. 2009). However, the first historical records of the Waorani occupying this area were in the early 20th Century, when reports of lethal spearing in the territory started. These lethal attacks on all outside intruders continued until first peaceful contact in 1958, and lethal spearings of outsiders by some Waorani living in voluntary isolation still occurs (Finer et al. 2009). From 1958 the majority of the Waorani were relocated, with the aid of missionaries and oil companies, to a single community called Tihueno on the western edge of their former territory. Although this relocation was nominally voluntary, the methods used by those who moved the Waorani were at times questionable. A polio epidemic occurred in Tihueno in 1969, killing and handicapping many of the Waorani population, and many Waorani left the community as they found the Waorani leaders in the community overbearing (Stoll 2002).

Families that left Tihueno founded new communities in the ancestral homelands of the Waorani, which now form Yasuní National Park and the Waorani Ethnic Reserve.

2.7 Traditional lifestyle of the Waorani

Before Western contact, the Waorani lived in small, highly-mobile family groups which moved between hilltop longhouses built on terra firme (Rival, 2002). The population was estimated at approximately 600 in the late 1950s and lived throughout the area which is now Yasuní National Park and the Waorani Ethnic Reserve. Before contact, the Waorani had a reputation with surrounding communities for fiercely defending their territory from non-Waorani intruders. This fierce reputation is still preserved by some Waorani subgroups, which refused Western contact and still live in voluntary isolation in the south and east of Yasuní National Park. These groups – the Tagaeri and Taromenane – who still follow a traditional lifestyle have been responsible for the lethal spearing of illegal loggers within their territory (Proaño García and Colleoni 2008). Historically, the Waorani attacked all outsiders, as they believed all non-Waorani were cannibals which would feed on humans (Rival, 2002). This practice cut the Waorani off from surrounding ethic groups, and is likely to be responsible for the uniqueness of their language – Wao terero, which is not related to any known language family – and their genetic isolation and homogeneity (Gómez-Pérez et al. 2011).

Within this isolated culture, each Waorani longhouse distinguished between Warani – people who were recognised as Waorani, but with whom the household did not have close relations, and their own longhouse and related longhouses (Waomoni). As the Waorani believed that most deaths were caused by Warani individuals, spearing raids between households were common, and up to 42% of deaths were a result of intra-tribal spearing (Beckerman et al. 2009). Unlike many other similar Amazonian communities, women and children were also killed during warfare, which may account for the small population size of the Waorani on first contact (Rival, 2002). This intra-tribal warfare also meant the Waorani frequently moved the location of their longhouses to avoid revenge killings (Rival, 2002). The Waorani used few cultivars, mostly collecting wild foods from the forest. Based on terra firme and avoiding the riverine areas around their territory where non-Waorani groups were settled, fish played a less important part in traditional Waorani diet than terrestrial animals and wild plants. Hunting technology was limited to hardwood spears and blowpipes whose arrows were tipped with curarae poison. These hardwood spears were used to hunt white-lipped peccaries (*Tayassu pecari*), and the blowpipe was used to hunt monkeys and birds. Other species, such as the tapir (*Tapirus terrestris*) and capybara (*Hydrochaeris hydrochaeris*), were considered taboo and were not eaten (Rival, 2002).

2.8 Specific study area within the Ecuadorian Amazon

This study was conducted in the north-west of Yasuní National Park at around 0°40'S,76°24W during April to June 2009, October 2009 to January 2010, March to August and October to December 2010. Two main sites close to the Rio Tiputini were used to study primate behaviour (Figure 2.4). The area around the Yasuní Research Station (YRS), managed by La Pontificia Universidad Católica del Ecuador, has high hunting pressure and is easily accessed by road (the maximum journey time from any community to the research station is 40 minutes by bus). In contrast, Tiputini Biodiversity Station (TBS), managed by Universidad San Francisco de Quito, is only accessible by a 2-3 hour boat journey from the nearest road. This area is not thought to have been actively hunted since the station was founded in 1994, and no hunters have been observed nearby. It is impossible however, to say that there is no hunting near this station, and thus it is classified as “low hunting pressure”.

Information on human hunting behaviour and perceptions of primates was gathered from three Waorani communities located on the Maxus Road, and between 5 and 30 km from YRS. In the early 1990s, the Maxus road was built south into Yasuní National Park from the River Napo, to allow the company Maxus to access their oil extraction facilities. Guyiero (located at the 32km mark on the Maxus road) was founded by a family group around 1994. As the family grew, some branches founded new communities nearby: Timpoca, which is located 9km down a side road that leaves the main road at approximately the 43km mark, and Kilómetro 36, which is located at the 36km mark. Therefore, the three study communities are essentially three related extended families, and each community had 3-15 adults (over the age of 16) permanently resident during the study period. All three are located within the boundaries of

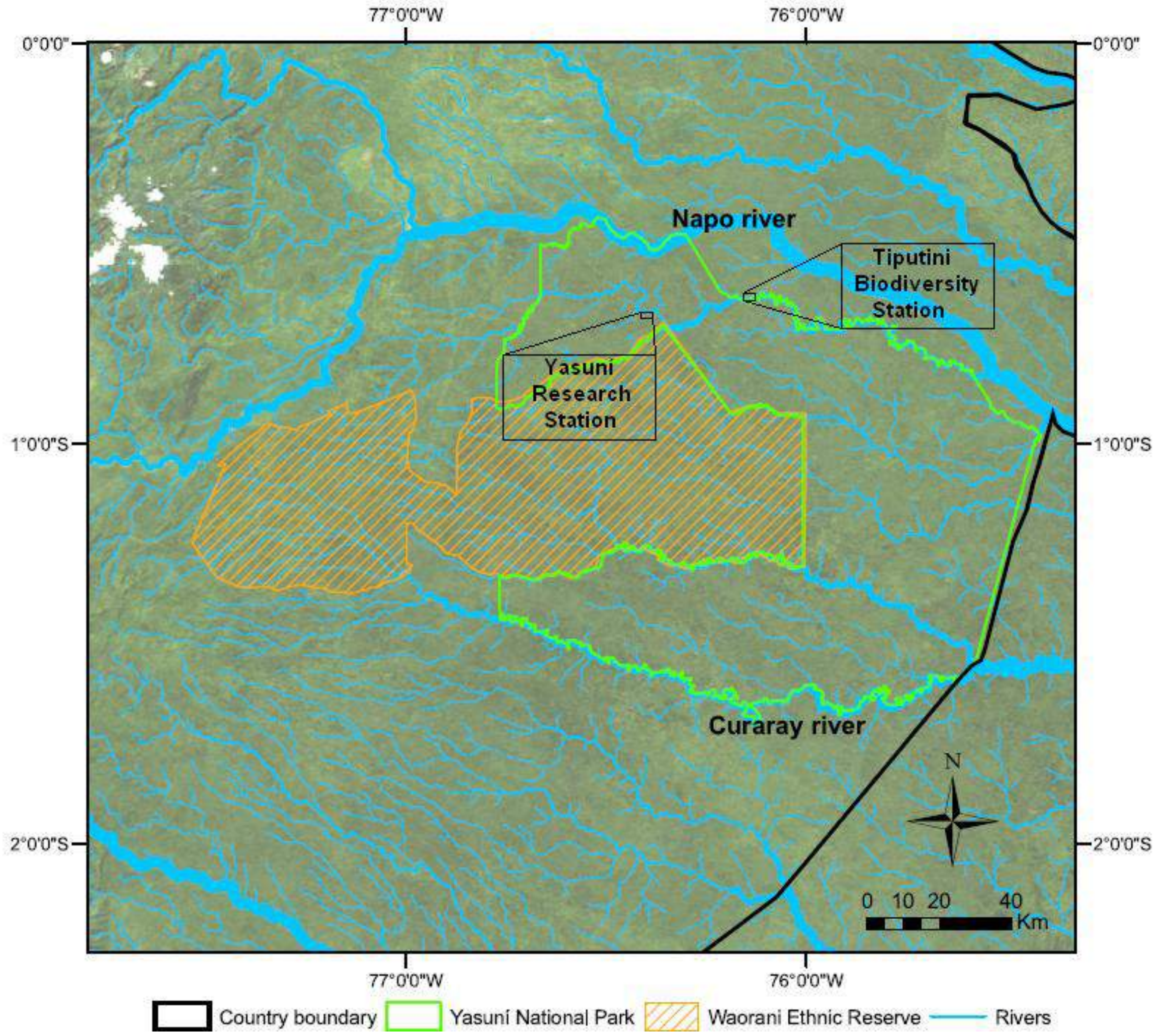

Figure 2.4. The locations of Yasuní Research Station and Tiputini Biodiversity Station in Yasuní National Park. Map adapted from Finer et al. (2009).

the national park and by water sources (either the Tiputini or Bogi River). Those who own canoes can gain easy access to large parts of forest using these rivers, and Texaco (the company who currently own the contract for oil facilities on the road) provides bus transport along the road for all three communities. This bus is used for visiting friends and relatives, as well as to gain fast access to areas of forest far from an individual's community, and to transport surplus meat to market (Franzen and Eaves 2007). Residency in the communities is very fluid, with relatives and friends visiting for extended periods (up to 9 months on one occasion during the study), and members of the community likewise taking extended visits to other communities.

Life in these communities does differ from the traditional way of life described above, though many similarities remain. Communities are still based on extended families, and matrilocal residency after marriage is still common. Although the oil company has built concrete houses in the communities, traditional structures made from palms are still used, and are considered preferable by many individuals as they have better ventilation. Each family uses one or two structures; those with two usually use one for cooking and socialising, and the other for sleeping.

The primary language is Wao terero, though most people speak some Spanish, and younger generations (under 50) are fluent in Spanish. The primary school in Guiyero provides bilingual education, with younger students taught in Wao terero and older students in Spanish. Most younger individuals (under 50) have some primary education, though few have secondary education. In order to receive secondary education, individuals must leave the communities and live in distant towns. Some individuals are aware of Christian teaching, but traditional beliefs and stories are still widespread. No one during the study self- identified themselves as Christian and many rejected Christianity as an outside religion.

2.9 Current subsistence activities in the study area.

Many individuals participate in the cash economy, either by selling wildmeat or handicrafts in the local market or through occasional work for the oil company, either as grass cutters or aiding construction work. This money is used to buy food items such as rice, coffee or sugar, and also pay secondary school fees. Individuals in the communities do not pay rent, primary school fees or for travel within the park. The majority of activities by individuals in the communities are part of a subsistence economy based on small scale farming, hunting and gathering. Women tend crops, mostly yuca and plantain, in small forest clearings. Generally, the forest is clear by the men of the household by cutting trees and controlled burning of the area. The women then plant and harvest the crops. Women also collect wild fruits, plants and honey from the forest, and palms and seeds to make hammocks, baskets and other handicrafts. Some households keep chickens, but no other livestock is kept. Children accompany their parents when they go to tend crops, hunt and gather, and older children also go on forest trips alone.

Although children start learning to hunt small birds with half or three-quarter size blowpipes and Waorani hunting is still predominately for subsistence (Franzen, 2006), many have changed their hunting methods from traditional spears and blowpipes to guns and dogs (Franzen, 2006; Mena V et al., 2000). Hunters are also now hunting species that were previously considered taboo, such as the tapir (*Tapirus terrestris*) (Rival 1993). Although men are the main hunters, some women also hunt, though this is usually opportunistically, such as killing animals with a machete when encountered near the community. Although women no longer actively hunt, many accompany their husbands while they hunt. All males over 18 go hunting, though the frequency with which they do this depends on various factors, such as the number of other adults males in their household and their position within the household. Additional information on current Waorani hunting is provided in Appendix 1.

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Chapter 3

The place of primates in Waorani ethnobiology: Implications for conservation

3.1 INTRODUCTION

3.1.1. Ethnobiology and local ecological knowledge

Ethnobiology is the study of particular ethnic groups' knowledge and relationships with plants and animals (Anderson 2011). Folk taxonomy, the way cultures name and categorise animals and plants, originally formed the core of ethnobiology (Hays 1983), but the discipline has diversified, incorporating elements of anthropology, biology, archaeology and medicine. Ethnobiological methods are also increasingly being adopted in diverse disciplines. In conservation, "traditional ecological knowledge" (TEK), has its roots in ethnobiology, but more focus is placed on traditional management practices (Nelson 2005), and their potential use for conservation. Local and indigenous ecological knowledge (LEK and IEK respectively) have been proposed as alternate terms to refer to this body of knowledge, as although TEK and IEK imply knowledge development through historical time, all knowledge should be understood as contemporary in nature (Stevenson 1996; Gilchrist et al. 2005). This paper will use the term LEK in order to recognise that such knowledge is contemporary, and may be held by non-indigenous peoples. Knowledge gained from LEK is often emic, documenting phenomena from the participants' perspective, whereas conservation science has traditionally valued etic perspectives based on empirical and outsider observations (Drew and Henne 2006). However, the combination of these two perspectives has led to numerous successful conservation projects based on LEK, such as defining species' biogeographical ranges (Gagnon and Berteaux 2009), and supporting forest conservation (Becker and Ghimire 2003).

Ethnoprimatology is a subsection of ethnobiology which aims to understand the interconnections between humans and other primates, often with the ultimate aim of informing conservation (Fuentes and Hockings 2010), and thus has many overlaps with LEK.

Ethnoprimatological studies contrast with traditional research on wild primates, in that humans are viewed as an integral part of the primate ecosystem, rather than a source of disturbance or “unnatural” behaviour (Fuentes 2006; Riley 2006). When ethnoprimatology was first proposed by Sponsel in 1997 as an important area for investigation, she suggested that

“the natural place to begin is with those indigenous societies, such as the Waorani, for which monkeys are an important species in the diet”

(Sponsel, 1997, p159).

3.1.2. The Waorani

This chapter focuses on the Waorani, and their perceptions of primates. The homeland of the Waorani is in Amazonian Ecuador, bounded to the north by the Napo River, and by the Curaray and Vilano Rivers to the south (Figure 3.1, Cabodevilla, 1994). This area is now part of Yasuní National Park and Waorani Ethic Territory, and the Waorani people have collection rights for all above ground resources (Finer et al. 2009), though it is illegal for these resources to be transported and sold outside the park. Traditionally, the Waorani were hunter-gatherer-farmers, growing a small number of cultivars in cleared forest, collecting wild plants and hunting mostly large monkeys and white-lipped peccaries (*Tayassu peccary*). Since first

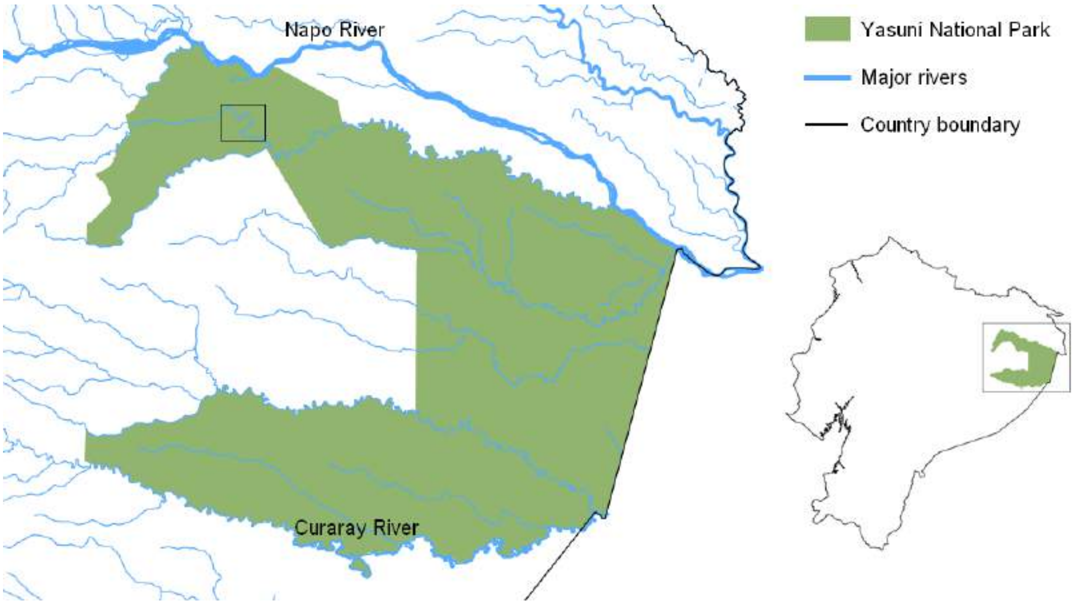

Figure 3.1. Location of study site in Ecuador and Yasuní National Park.

western contact in 1950, some Waorani have moved to permanent settlements, often centred around a school. Currently, there are around 2000 Waorani living in approximately 38 small scattered villages, and small groups scattered throughout the forest, pursuing more traditional ways of life (Lu 2001; Beckerman et al. 2009; Finer et al. 2009). Some communities related to the Waorani (the Tagaeri and Taromenane) living within Yasuní National Park have refused all western contact and pursue entirely traditional lifestyles (Finer et al. 2009), with the exception of some integration of some western material goods, such as using plastic tape (found in abandoned oil facilities) on traditional spears (Proaño García and Colleoni 2008).

Waorani hunting is still predominately for subsistence; Franzen (2006) estimated that only around 4% of all wildmeat extracted by three communities in the north of Yasuní National Park is sold at a local market outside the park by the Napo River. Since first western contact, however, many Waorani have changed their hunting methods from traditional spears and blowpipes to guns and dogs (Franzen, 2006; Mena V et al., 2000). Hunters are also now hunting species that were previously considered taboo, such as the tapir (*Tapirus terrestris*) (Rival 1993). The Waorani maintain a largely traditional lifestyle, but use of forest products has declined, with families increasingly consuming food bought in markets (Franzen and Eaves 2007). Although international interest in the Waorani, Tagaeri and Taromenane has always been high, interest in these communities as actors in political and conservation events is likely to increase with the Ecuadorian Government's Yasuní-ITT initiative: the Ecuadorian government requests compensation from the international community in return for protecting the Isthpingo-Tiputini-Tambococha (ITT) petroleum block of eastern Yasuní National Park from future oil extraction (Finer et al. 2009).

Although the Waorani of the Ecuadorian Amazon have been well studied and have a high profile internationally (Finer et al. 2009), no detailed research has been conducted specifically on contemporary Waorani perceptions of primates and other animals. Some ethnographic accounts do document some aspects of Waorani culture which relate to primates. For example, the Waorani are reported to specialise in hunting monkeys and birds (Rival 1996), Waorani women have been observed to breast-feed infant monkeys (Rival, 2007), and “monkey houses” were traditionally constructed close to the longhouse (Mondragon & Smith, 1997). However, these are anecdotal reports of single incidences, or reports of traditional Waorani culture. Although reports of the historic importance of primates to Waorani culture are important, the contemporary relationships, perceptions and interactions which are included with traditional perspectives in LEK, have greater potential for conservation.

This study focuses on three small communities in Ecuadorian Amazon, and aims to place primates within the contemporary ethnobiology of the Waorani. The study aims to describe the cultural importance of species present in the area, specifically addressing how the Waorani within the study site conceptualise and categorise the group of animals which is known scientifically as the order *Primates*. Describing species categorisation is the domain of folk taxonomy, but this study will also investigate consumption, perceived dietary overlap and cultural salience of primate and non-primate species. The conservation implications of findings are discussed, including methodological insights to support the use of LEK and ethnobiology for conservation projects.

3.2. METHODS

3.2.1. Study communities

Data collection was carried out inside Yasuní National Park, Ecuador, in communities located along the Maxus road (Figure 3.1). The Maxus road is one of two main oil roads entering the Yasuní National Park from the north, and is used to access the communities of Guiyero, Kilómetro 36 and Timpoca, which participated in this study (Figure 3.2). The road was built in 1994 and was soon after colonized by people from the Waorani and Quichua ethnic groups. The oil company provides a bus service to Pompeya by the river Napo for members of the community to visit the weekly market, and a bus service at least twice daily between the three communities during the week to allow children to attend the primary school in Guiyero. The primary school is also funded by the company, and the Waorani use the oil company medical centre, located at the largest oil extraction facility in Figure 3.2. There has been no colonisation by other ethnicities, excepting individuals who marry Waorani and come to live in the communities with their spouse.

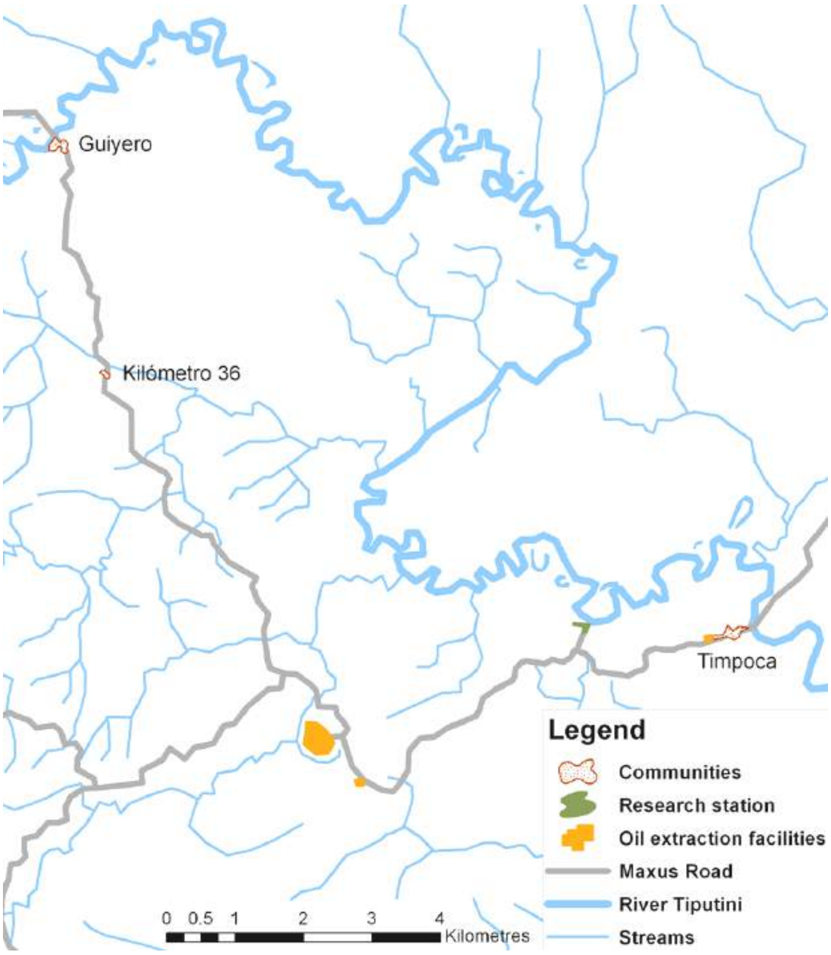

Figure 3.2. Communities included in this study and their location relative to the Maxus Road and its oil extraction facilities.

3.2.2. Data collection

Interviews

Twenty-seven interviews with 35 Waorani participants from 11 households were conducted between April and December 2010 in the three communities (Table 3.1). All willing adult members of the three communities were interviewed, which represented 28 of 39 adults (aged over 16) who were permanently resident during April – December 2010, and three long-term Waorani visitors (resident for longer than two months). All individuals in the community were invited to take part in the study. Although no-one directly refused to take part, those who did not participate asked me to return later when they were free. After two such requests from each individual, I asked them to contact me when they were free, as I understood this may be an indicator of an unwillingness to participate. Eleven individuals did not subsequently contact me during the study period.

Table 3.1. Number of participants from each community, divided by age and sex

Age and sex of participants	Number of participants from each community			Total number of participants
	Guiyero	Timpoca	Kilómetro 36	
Children aged 12-15	2	1	1	4
Males aged 16-50	6	7	1	14
Females aged 16-50	12	3	2	17
Total	20	11	4	35

Interviews consisted of four sections and were semi-structured, allowing new questions and topics to be discussed in response to individual responses. Interviews were conducted with single individuals where possible, but on some occasions additional individuals were present and contributed to all or part of the interview. Four individuals who were present but not the intended interviewee gave personal answers about their preferred species and these were included in analyses. For three interviews, two sections of the interview were excluded from analysis (focal animal identification and pile sorting) as multiple individuals were present and it was not possible to assign animal identification to a single individual. Inclusion of these interviews would have created an upward bias in the probability of identification and consumption. As not all individuals who were present answered all questions, sample size varies for each section. All interviews were conducted in Spanish, but on two occasions younger family members were present to act as translators for individuals who did not speak fluent Spanish. All interviews were recorded with a Marantz PMD661 Professional Portable SD Field Recorder. Interviews were later transcribed. Animal names which were not recognised during transcription where identified during informal discussions with informants in December 2010. Spanish words which were unknown were translated by an English speaking Ecuadorian.

Section 1: Free listing

Participants were asked to list the names of all the animals they knew, as a means of placing primates within the broad context of ethnozoological knowledge. Free lists can be used to calculate the cultural salience of named species (Bernard 2006). Cultural salience refers to the importance of an item in the studied community. It is assumed that more important items will be mentioned earlier, and by more individuals during free-lists. This activity was carried out with all individuals, but the resultant list was only included in the analysis if other individuals present did not contribute to the list, to avoid contamination (Quinlan 2005). Eighteen free lists were available for analysis. For animal names in the local language Wao terero, the spelling of previous publications has been followed where these are available (authority from Rival, 2002 in cases of conflict). For animal names in Wao terero for which no previously published record could be found, spelling follows the orthographic rules laid out in Rival (2002, xxiii), although some sounds used in animal names were not included in this key. In these cases, spelling followed English spelling rules.

Section 2: Identification and consumption of specific species

To investigate recognition of key species in the area, and investigate Waorani consumption of these species and perceptions of dietary overlap, each participant was shown photographs of 18 common mammal species in the study area (full list in appendix 2). These 18 species included all 10 primate species, the four most commonly consumed ungulates. The capybara (*Hydrochaeris hydrochaeris*) and tayra (*Eira barbara*) were also included as common mammal species of a similar size which were rarely consumed (according to Franzen, 2006). The kinkajou (*Potus flavus*) and olingo (*Bassaricyon alleni*) were included as previous research suggested these species may be categorised as primates by lowland neotropical cultures (Lizarralde 2002; Urbani 2006). If an individual recognised the animal, they were asked to give its name, whether they had eaten it and what the animal ate. During this section, participants gave additional information about the species, and additional questions were asked when appropriate. Decoy primates which were not present in the study area were also presented to each individual to validate the assumption that people were indeed aware of the species in their area, rather than guessing. These decoy species were the black and white colobus (*Colobus guereza*) and De Brazza's monkey (*Cercopithecus neglectus*) from east Africa, golden lion tamarin from the Atlantic forest of Brazil (*Leontopithecus rosalia*), and the uakari from Amazonian Brazil (*Cacajao calvus*). The black and white colobus was removed as a decoy species, after it was misidentified as the giant anteater (*Myrmecophaga tridactyla*) in five out of five interviews. This misidentification is likely partly due to the presence of lighter stripes down the torso of both species, and their long tail hair. The remaining three species were stated to be unknown by 20 of 26 participants. One young woman identified the uakari as a spider monkey (*Ateles belzebuth*). However, she also correctly identified the photo of the spider monkey when presented with the image. Six individuals stated they did know one or more of the decoy species, but were not able to name them, because the photo showed a different type of monkey to the species they knew in the area. Decoy species were not included in the analysis.

Section 3: Pile sorting

Free pile sorts are used to investigate how a group of people classify a certain group of objects (Bernard 2006). In order to understand whether primates were viewed as a distinct group, and how primates were perceived to relate to other species in the area, participants were asked to sort the 18 species into groups of the animals they thought were similar. Participants were informed that they could group animals in any way they wished. Once informants had finished sorting the photos, they were asked to explain why they had created these groups. 24 pile sorts were conducted.

Section 4: Consumption behaviour

Although previous researchers working with the Waorani report that the woolly monkey (*Lagothrix poeppigii*) is the preferred species for consumption (Mena V et al. 2000; Rival 2002), no quantitative data have been presented to support this statement. Participants were asked their favourite species for consumption. Those individuals who did not name a primate were also asked their favourite primate species.

Wild plant consumption

Food diaries were used to determine which wild plant species were most frequently consumed by the Waorani, in order to compare perceived animal diets with actual diets of the participants. Although Waorani ethnobotany is well documented, and there is extensive knowledge on which species the Waorani perceive as edible (Mendoza Troya 1994; Mondragon and Smith 1997; Macía 2004; Freire Betancourt 2006; Rival 2009), the extent to which these wild plants are consumed by the Waorani and their relative importance is unknown. Between January and December 2010, informants from households in Guiyero, Timpoca and Kilómetro 36 recorded household consumption of wild food sources. During the year, data from 10 households was recorded, but inconsistencies in the records of three households meant the data were not included for analysis. Of the seven remaining households for which data were considered reliable, four households recorded data for the full year. One household dropped out of the study in August 2010 when the family moved out of the study area. Two households joined the study in June and October 2010 respectively, when they moved into the study area. Each day, informants recorded whether the household consumed wild plants. Data were not recorded if the informant was staying away from the household, but information was recorded for a mean of 78% of possible days during the year in these seven households.

3.2.3. Secondary data sources

For all species mentioned during the freelisting exercise, information on the contribution to Waorani diet was taken from published literature to investigate the relationship between species consumption and cultural salience. During August to December 2002, all animals hunted in Timpoca, Guiyero and nearby Dicaro were recorded, and the total number of individuals and the weight in kilograms is presented in Franzen (2006). This information was used to determine the contribution of different species to the diet of the communities. Mean weight for each species was also derived from this information, except where the species was not recorded as hunted, when weights were taken from Emmons (1999).

Information on trade with non Waorani communities was used to investigate the impact of trade on the language used to refer to the 18 focal species. From January 2005 to May 2007, wildlife passing through Pomeya market was recorded by Suárez et al. (2009), and it is in this market which the Waorani of the study communities sell wildmeat to non-Wao terero speakers. The volume of trade for each species at the market was used as a proxy for the likelihood that members of the communities needed to use non-Waorani names for species. A median of two individuals per focal species were observed in the market (range: 0-391 individuals), so species were split into two roughly equal groups; two or less individuals observed in the market (10 species), or three or more observed (eight species).

In order to examine the relationship between Waorani and western scientific perceptions of focal species diets, information on the diet of four species of primate in Yasuní National Park was taken from the literature (Di Fiore 1997; Kostrub 2003; Carrillo-Bilbao, Di Fiore, and Fernández-Duque 2005; Dew 2005; Suarez 2006). Information on these studies can be found in Appendix 2. Comparable information on the diets of the other 14 focal species was not available.

3.2.4. Data analysis

Perceived similarity of primate and non-primate species

For each of the 18 focal species, the proportion of the 24 pile sorts which placed the species in each of four group types was calculated; in a group with only primate species, in a group with only non-primate species, in a group with primate and non-primate species, or in a group alone. This information was used to examine the perceived similarity of each species to the scientific group *primates*.

For each dyad of two focal species (153 dyads in total), the number of pile sorts in which both species were placed in the same pile was calculated. Wilcoxon rank sum tests (identical to a Mann Whitney U test) were used to compare the number of co-occurrences in a single pile by three types of dyad: primate:primate (p:p), primate:nonprimate (p:n) and nonprimate:nonprimate (n:n). Boniferoni corrections were applied as multiple tests were conducted on the same data set, reducing the significant P level to 0.025. Dyads which were placed in the same group in the majority of pile sorts (13 or more) were also identified, and assumed to be perceived as more similar than those which were less often placed together.

Cultural salience

Free lists were used to calculate the cultural salience of the animals listed. Calculations of cultural salience have two assumptions; 1) items named by more individuals are more salient (in this case, more central to the concept of "animal"), 2) items named earlier on an individual's list are more salient (Quinlan 2005). The following equation (from the calculation method specified by Quinlan, 2005) was used to calculate the salience of each animal mentioned by an individual:

$$\text{Salience} = \frac{1 + length_i - position_i}{length_i} \qquad \text{eqn 3.1}$$

Where *length* is the number of animal names given by individual *i*, and *position* is the location of a specific animal in the list of individual *i*, for example, the first named animal is position 1, the second named animal in position 2 etc. If an animal is not mentioned by an individual, its salience is zero. The cultural salience of each animal is calculated using the following equation:

$$\text{Cultural salience} = \frac{\sum Salience_i}{n} \qquad \text{eqn 3.2}$$

Where *n* is the number of individuals which participated in a study. Cultural salience for each animal named during free listing was calculated using the program ANTHROPAC (Borgatti 2012). Multiple names for single animals were grouped for analysis. All participants were to some degree bilingual in Wao terero and Spanish, but Quichua names for animals were also frequently given.

Determinants of cultural salience

Any mammal species which was mentioned either during free listing or in Franzen's 2006 paper describing Waorani diet in the study communities was included in an analysis of the determinants of cultural salience, as calculated above. Only named animals which corresponded to a single species were included in analysis. For example "ardilla" or squirrel, named by two individuals, was excluded as there are numerous squirrel species present in the area. This meant eight animal names were excluded, none of which were given by more than four individuals. In order to reduce bias in results, species recorded by Franzen (2006) as hunted, but which could be included in these broad animal categories (i.e. *Sciurus igniventris*, northern Amazon red squirrel) were also excluded from analysis.

It was hypothesized that species would be more culturally salient if they had larger body sizes, were more frequently consumed or traded by the Waorani, or if they were primates. Species with larger body sizes may be more obvious in the forest, and will also feed families for longer, which may increase their salience. On the other hand, the largest species are not necessarily those which are most consumed, and species may be more salient as they are often seen in households. Alternately, species may be more salient as they are more often traded and therefore contribute to the cash economy of a household. Finally, primates were included as a predictor to examine whether primates are considered important by the Waorani. Dietary contribution of each species and mean weights for hunted species in the area were taken from Franzen (2006). When weights for species were not available, median weight for the species was taken from Neotropical Rainforest Mammals: A Field Guide (Emmons 1999). Species weight and two measures of dietary contribution (number of individuals and total meat weight) were highly correlated – initial analyses indicated that dietary contribution as measured by number of individuals best explained the variation in cultural salience, and so only this measure was included in the final models. Generalised linear models were considered for analysis as cultural salience is bounded at 0 and 1, suggesting analysis for proportion data would be appropriate, but cultural salience did not conform to the distributional expectations of proportion data. A linear model provided a better fit for the data and residuals. Analyses were conducted in R 2.14.1 (R Development Core Team 2008), and used the package 'MuMIn' to calculate ΔAICc and model weights. Models with ΔAICc<4 are presented in the results, and all possible models in Appendix 2. Two models had almost equal support (Weight = 0.32 and 0.31), but the results of the simpler model are presented in the results, as the additional variable in the more complex model was not significant and had a negligible effect on model fit.

Perceived dietary overlap

Wild plant foods eaten by the Waorani and those named as consumed by focal species were identified using published accounts of Waorani ethnobotany (Mendoza Troya 1994; Mondragon and Smith 1997), and confirmed by Álvaro Pérez Castañeda, botanist and project coordinator of the Yasuní Forest Dynamics Plot. Wild plants, domesticated plants and some insects and animals were named as food items consumed by focal species. These food items were classified as "consumed" or "not consumed" by the Waorani, depending on whether the item appeared in food diaries during the study. As the food diaries are not 100% complete for the year, some food items may be mistakenly identified as “not consumed”.

To control for differences in the number of species reportedly eaten by each focal species, proportions were used to compare perceived dietary overlap between the Waorani and primate and non-primate species. The total number of participants who named each food item for each focal species was calculated. The number of participants who mentioned each “consumed” item was summed for each of the focal species, as was the total number of participants who mentioned each “not consumed” food item. For each focal species, the percentage of the named food items which were consumed by the Waorani was calculated. To compare these percentages between primates and non-primates, a Wilcoxon rank sum test was used.

To investigate the impact of Waorani consumption of perceptions of wild animal diets, the total number of mentions for each wild plant species consumed by the Waorani in this study and the total number of wild plant species not consumed by the Waorani were calculated across all participants for all focal species. Wild plants consumed by the communities during this study were compared with those which were not using a Wilcoxon rank sum test.

Dietary preferences

For each individual, preference scores were assigned to each animal species named as a preferred species for eating, where:

$$species\ score = \frac{1}{number\ of\ species\ named\ by\ individual} \qquad \text{eqn 3.3}$$

Therefore, if an individual named a single species when asked which species they preferred, the species was given a score of one. If a species was not listed, it received a score of zero. If an individual named multiple species, each species named was assigned a fraction score. The sum of scores across all individuals was calculated for each species named.

3.3. RESULTS

3.3.1. Species names and language used

Participants referred to all 10 primate species in the area as *monos* (Spanish, *monkeys*), for example "*mono maquisapa*" for the spider monkey, suggesting that primates are seen as a group. However, they also referred to the olingo (*Bassaricyon alleni*) and kinkajou (*Potus flavus*) as *monos*. During interviews, participants informed me there were three *monos nocturnos* (Spanish, *nocturnal monkeys*): *gamönga*, *amönka*, and *ganata* (Wao terero names). The noisy night monkey (*Aotus vociferans*) was consistently identified as *amönka* by 18 of 19 participants who assigned a name to the photo. Participants were approximately equally divided as to whether the kinkajou or olingo were *ganata* or *gamönga*, though the kinkajou was identified as *gamönga* by 9 participants, and *ganata* by 4, whereas the olingo was identified as *gamönga* by 7 and *ganata* by 6, with 5 using the names interchangeably. These inconsistencies in naming the olingo and kinkajou may lie in the difficulties in distinguishing these two species from photos alone – participants informed me that the main distinctions were their calls and size, with *gamönga* being bigger, providing further evidence that *gamönga* refers to the kinkajou, which is twice the weight of the olingo. During free listing, the three informants mentioning all three species all referred to them in the order "*gamönga*, *amönka*, *ganata*". One further individual mentioned "*amönka*, *ganata*". This highly consistent ordering provides further suggestion that these three species are a culturally cohesive animal group.

The most recognised species were the white lipped peccary, red brocket deer (*Mazama americana*) and woolly monkey, but all species were recognised by at least two thirds of participants. However, some species were frequently confused, in particular, the olingo and kinkajou (Figure 3.3). Other species which were confused were the two peccary species, and the titi monkey (*Callicebus discolor*) and howler monkey (*Alouatta seniculus*). Names for species were given in Spanish, Wao terero and Quichua, with many participants giving multiple names in different languages for a single species. Nevertheless, all species were most frequently named in Wao terero, with the exception of the red brocket deer, which was most frequently named in Spanish, and the white lipped peccary and collared peccary (*Pecari tajacu*), which were equally likely to be named in Wao terero or Quichua. The 10 species for which two or fewer individuals were traded in Pompeya market during (see appendix 2 for

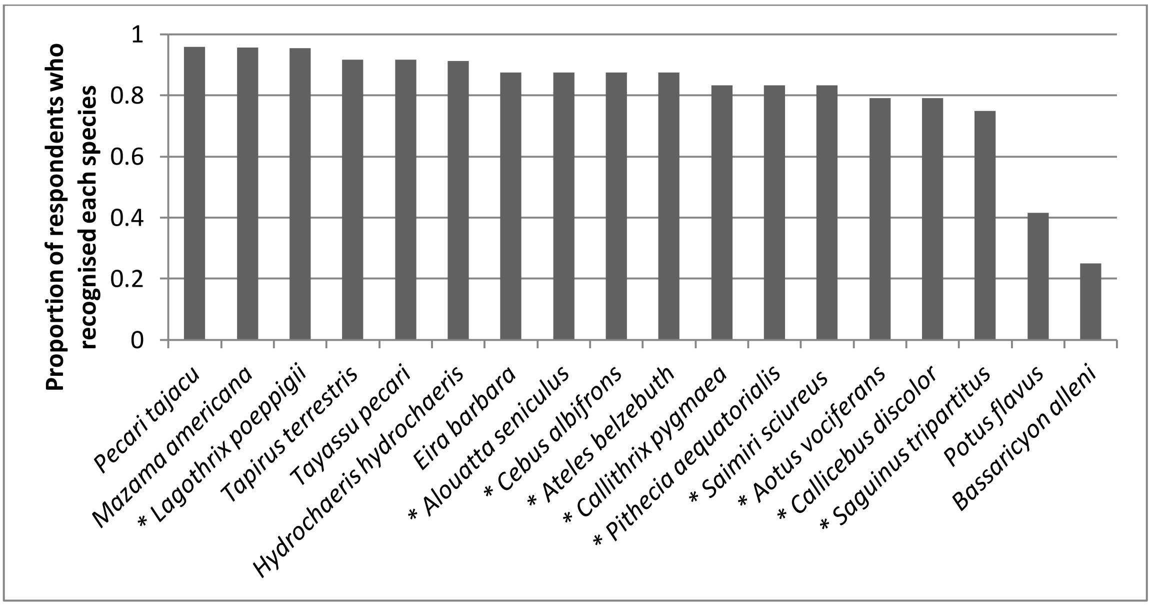

Figure 3.3. Proportion of 24 participants who recognised and correctly named each of the 18 focal species. Primate species are indicated with an asterisk (*). Potus flavus and Bassaricyon alleni were only considered correctly named when referred to as gamönga and ganata respectively.

volumes), where more likely to be referred to in Wao terero than those with more than 2 records in the market (Wilcoxon rank sum test, N_{high} = 8, N_{low} = 10, W = 10.5, p=0.009).

During free-listing, individuals named an average of 16.5±SD11.7 animals (range 4-51). Eleven animal names during the free listing process could not be assigned to a specific animal by myself or informants, and were perhaps mispronunciations, mistakes or uncommon animals. These names were given by single individuals. A further 142 animal names were given, only one of which was neither a bird nor mammal, *tortuga* (Spanish, tortoise). All animals named were wild and indigenous to the area – no domestic animals were named. Names for birds included specific names for a single species e.g. *tuvè* (Wao terero) for the mealy parrot (*Amazona farinosa*) and general names for a group of birds e.g. *loro* (Spanish, *parrot*). Most names given for mammals were species specific, with the exception of *mono* (Spanish, *monkey*), which participants used to refer to both the woolly monkey (*Lagothrix poeppigii*), and as a descriptor for all monkeys. When participants stated *mono* as a species, they were asked during the interview to clarify what they referred to, and usually confirmed they were talking about woolly monkeys by stating *mono mismo* (Spanish, *monkey itself*) and giving an alternate name for the species (either the Quichua *chorongo* or Wao terero *gata*). In Wao terero, the first language of the participants, *gata* is the name of both the woolly monkey and monkeys as a group, which is likely to be the reason for participants referring to woolly monkeys simply as “monkey”. Multiple names for the same animal (in Spanish, Quichua and Wao terero) were collapsed, thus the 142 names referred to 83 animals or animal groups. For example spider monkeys were referred to as *deye* (Wao terero), *maquisapa* (Quichua) and *mono araña* (Spanish), but are included in the analysis as a single species referred to by 11 individuals. Analysis is focused on the 31 named mammals which referred to single species.

3.3.2. Is the scientific family *primates* recognised as an exclusive animal group?

Two individuals did not make any groups, and stated that all animals were equal and different. Of those who did make groups, two principal explanations for the grouping were given. Firstly animals in a group spend time together and can be encountered together in the forest, or feed on the same foods. Alternately, animals were split into *arriba* (Spanish, *above*, that is tree dwelling animals) and *abajo* (Spanish, *below*, ground dwelling animals, sometimes referred to as *de pata*, Spanish, *of hoof/paw*). These individuals also identified a third group, *de pluma* (Spanish, *of feather*), which included all birds. The tayra was identified as a problem animal for categorisation by some individuals, as it spent time both in trees and on the ground.

During the pile sorting exercise, participants created a median of 5.5 groups (range 2 – 17, interquartile range), and the 10 primates were not grouped together by any individual. The most frequent group given which included any primate was 4 individuals who grouped the night monkey, olingo and kinkajou in a unique group. One individual grouped all diurnal primates in a single group. The most common group was the white-lipped peccary and collared peccary, created by 9 individuals. Most primates were more frequently grouped with other primates than most non-primate species were (Figure 3.4). The pygmy marmoset (*Cebuella pygmaea*) was less frequently grouped with other primates as it was placed in a group on its own in half (12) of the pilesorts. In contrast, the noisy night monkey was less frequently grouped with primates as it was placed in an exclusive group with the kinkajou, olingo or both in seven pilesorts. These groups with the noisy night monkey also contributed to the high proportion of pilesorts in which the kinkajou and olingo were grouped with primates.

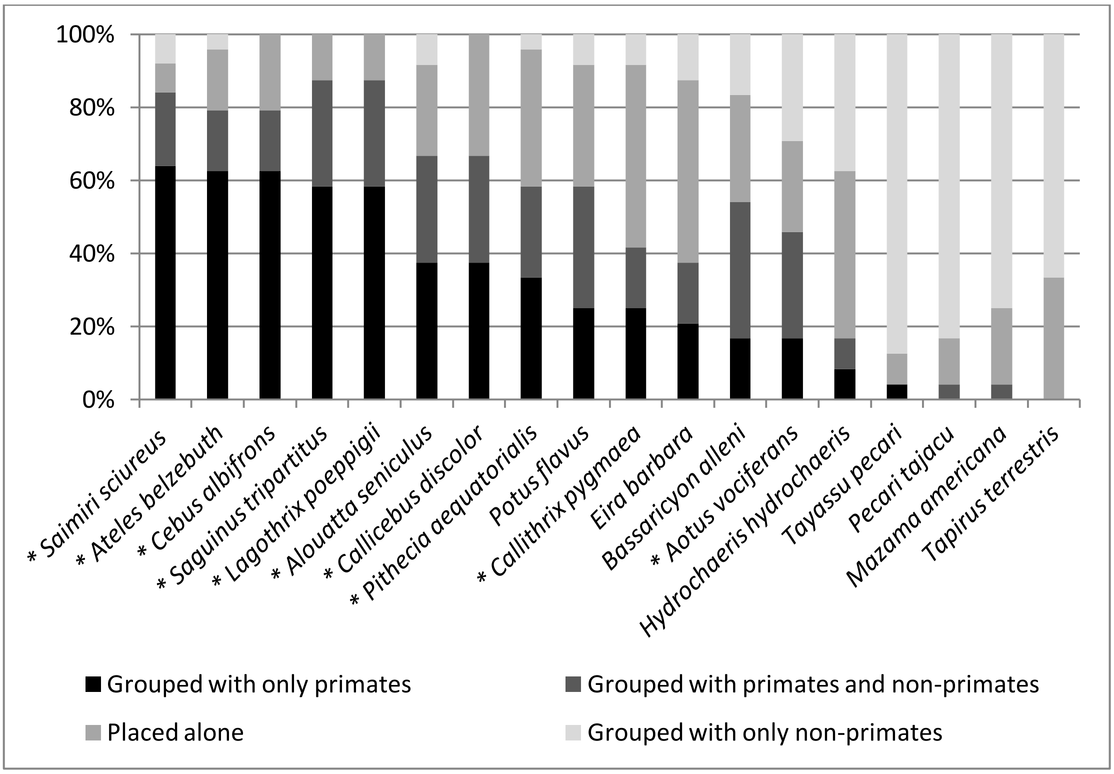

Figure 3.4. Proportion of pile sorts in which each of the 18 focal species is placed in a group with any primate, placed in a group alone, or place in a group only with non-primate species. Primate species are indicated with an asterisk (*).

During the pile sorting exercise, primate pairs co-occured in a median of 7 piles (interquartile range 6-10). In contrast, the majority of primate and non-primate dyad were never placed in the same pile (median of 0 piles, interquartile range 0-3) which is significantly fewer (Wilcoxon rank sum, $N_{p:p}=45$, $N_{p:n}=80$, W= 3484, P<0.001, Figure 3.5). Non-primate pairs co-occured in a median of 1.5 piles (interquartile range 0-7), which was not significantly more than the number of piles in which non-primates:primates dyads occurred (Wilcoxon rank sum, $N_{n:n}=28$, $N_{p:n}=80$, W = 855.5, p=0.047). All primate dyads were placed in the same pile by at least 3 participants. These results suggest that primates may be viewed as an exclusive animal group. However, this analysis includes only the subset of species in the area which were included as focal species.

Six species dyads were placed in the same pile by more than half of the participants, suggesting they are generally perceived as similar:

1) White lipped peccary and collared peccary (19 individuals)

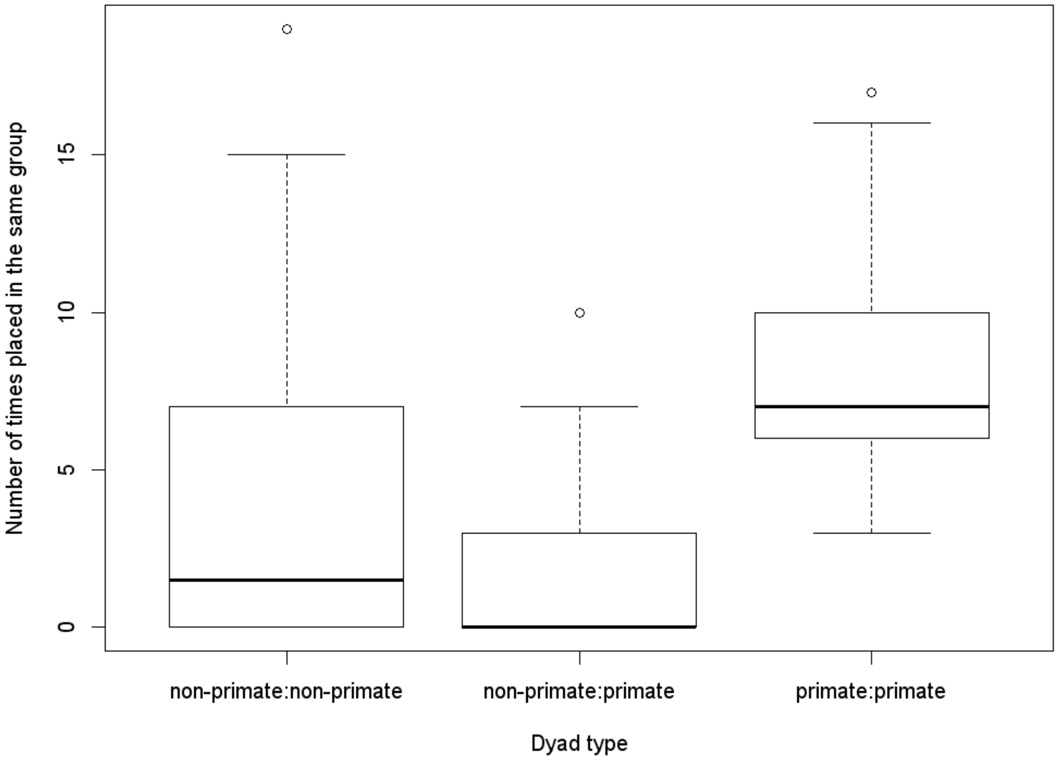

Figure 3.5. Number of times each dyad type occurred in the same pile during pile sorts.

2) Woolly monkey and spider monkey (17 individuals)
3) Squirrel monkey (*Saimiri sciureus*) and golden mantled tamarin (*Saguinus tripartitus*) (16 individuals)
4) Howler monkey and woolly monkey (15 individuals)
5) Red brocket deer and tapir (15 individuals)
6) Howler monkey and spider monkey (13 individuals)

The primate:non-primate dyad most commonly placed in the same pile was the noisy night monkey and olingo, placed in the same pile by 10 individuals.

3.3.3. Perceived diet of focal animals, and overlap with recorded Waorani consumption of wild plants

In total, 68 plant items were named as being eaten by the focal species, of which 54 were wild plants, and 14 were domesticated. The most commonly mentioned non-plant item were *grillos*

(Spanish, *crickets*), though butterflies, worms, bird eggs, birds and bats were also mentioned. Numerous participants stated that the peccary species ate the same as each other and were very similar. Parallels between the diets of different monkey species were also reported. Few individuals stated that species ate the same food as humans, though many individuals named plants they also consumed as part of a species' diet. Numerous individuals spontaneously mentioned animals, coming and “stealing their food”, mostly yuca, plantain and bananas. The chief culprit was the tayra, who was also accused of stealing chickens by two individuals (Figure 3.6). With the exception of the pygmy marmoset and the capybara, the majority of dietary items reported to be consumed by focal species were also consumed by the Waorani, although individuals rarely explicitly acknowledged dietary overlap between themselves and the focal species. Across all species, a median of 63.3±12.2% of food items named were also consumed by the Waorani. There was no difference in overlap between primate and non-primate species (Wilcoxon rank sum, $N_{primate} = 10$, $N_{non\text{-}primate} = 8$, $W = 21$, $p = 0.1$).

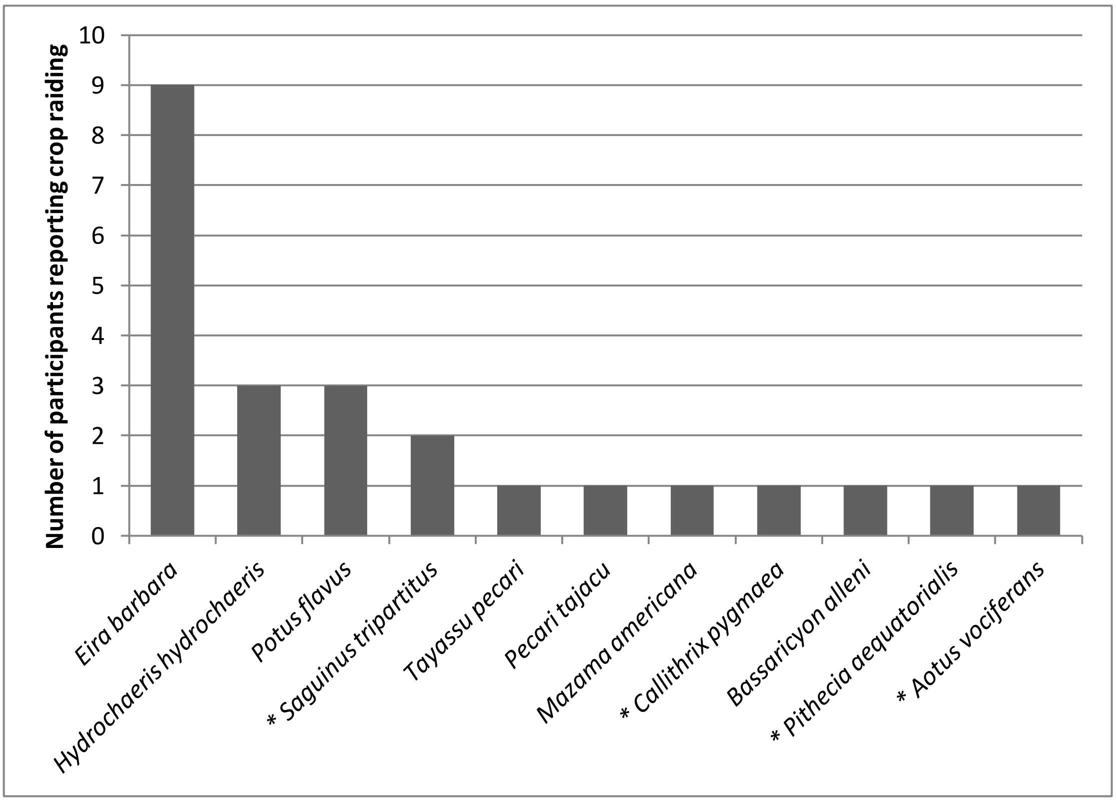

Figure 3.6. Focal species reported to raid crops. Primate species are indicated with an asterisk (*).

Wild plants which were eaten by the Waorani during the study period were named more often as food for animals than those which were not eaten by the Waorani (Wilcoxon rank sum, $N_{eaten} = 10$, $N_{not} = 44$, $W = 425$, $p < 0.001$, $median_{eaten} = 23.5$, $median_{not} = 1$). Of the four primate species for which published records of diet were available, participants identified the broadest diet for the spider monkey, reporting 10 different species, of which nine were consumed in the study period by Waorani (see appendix 2). Woolly monkeys, titi monkeys and golden-mantled tamarins were reported to consume a subset of these 10 species (Table 3.2).

Table 3.2. Species which participants reported were eaten by the four focal primates. Species names in bold were observed in the diet of the Waorani in this study. White cells indicate that one or more individuals reported the primate eating the corresponding plant species (shaded cells were not reported). The letters show the plants recorded in the literature as being components of the primates' diets: Species consumed (S); genus consumed (G).

	Spider monkey	Woolly monkey	Titi monkey	Tamarin
Astrocaryum chambira	S		▨	▨
Bactris gasipaes		▨	▨	▨ G
Cleidion amazonicum			▨	▨
Cecropia sciadophylla	S	▨ G	S	▨ S
Inga spp.	G	G	G	
Mauritia flexuosa				▨
Oenocarpus batava	S		▨	▨
Ochroma pyramidale		▨		▨
Pourouma cecropifolia	G	G	G	S
Theobroma spp.	S	G	▨	

3.3.4. Are primates culturally more important than other species?

Consumption

The 27 participants named 12 species as preferred species for consumption, the most popular of which was white lipped peccary (Figure 3.7). The white lipped peccary was also found by Franzen (2006) to be the most important contributor to the diet of the communities when measured by number of individuals and meat weight (45% of all meat weight). When asked about preferences within only monkeys, the overwhelming majority preferred woolly monkeys (preferred species for 13.5 of 24 individuals, Figure 3.8).

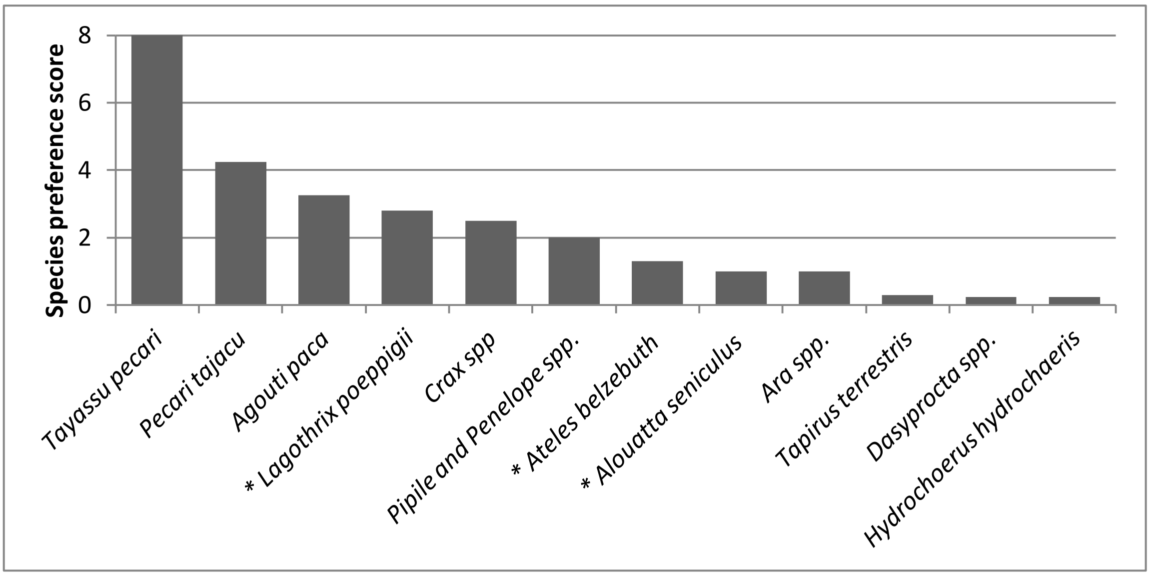

Figure 3.7. Preferred species for consumption by 27 participants. Primate species are indicted with an asterisk (*).

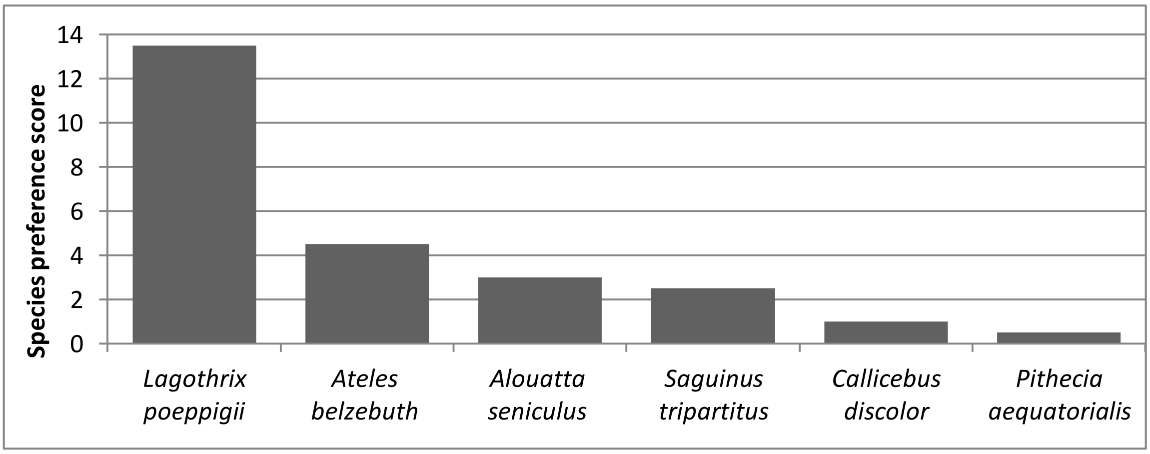

Figure 3.8. Preferred primate species for consumption.

All focal species had been eaten by at least one participant, with both species of peccary and the woolly and spider monkeys reportedly eaten by all individuals who correctly identified the species (Figure 3.9). Fewest individuals had eaten the pygmy marmoset, with the majority reporting they were just for pets, or were too small to hunt. The tayra had been eaten by approximately half the participants who recognised it, but tayra were rarely reported to be intentionally hunted; instead they were killed opportunistically when encountered raiding gardens. On some occasions the tayra was then eaten by the family, on other occasions it was fed to hunting dogs.

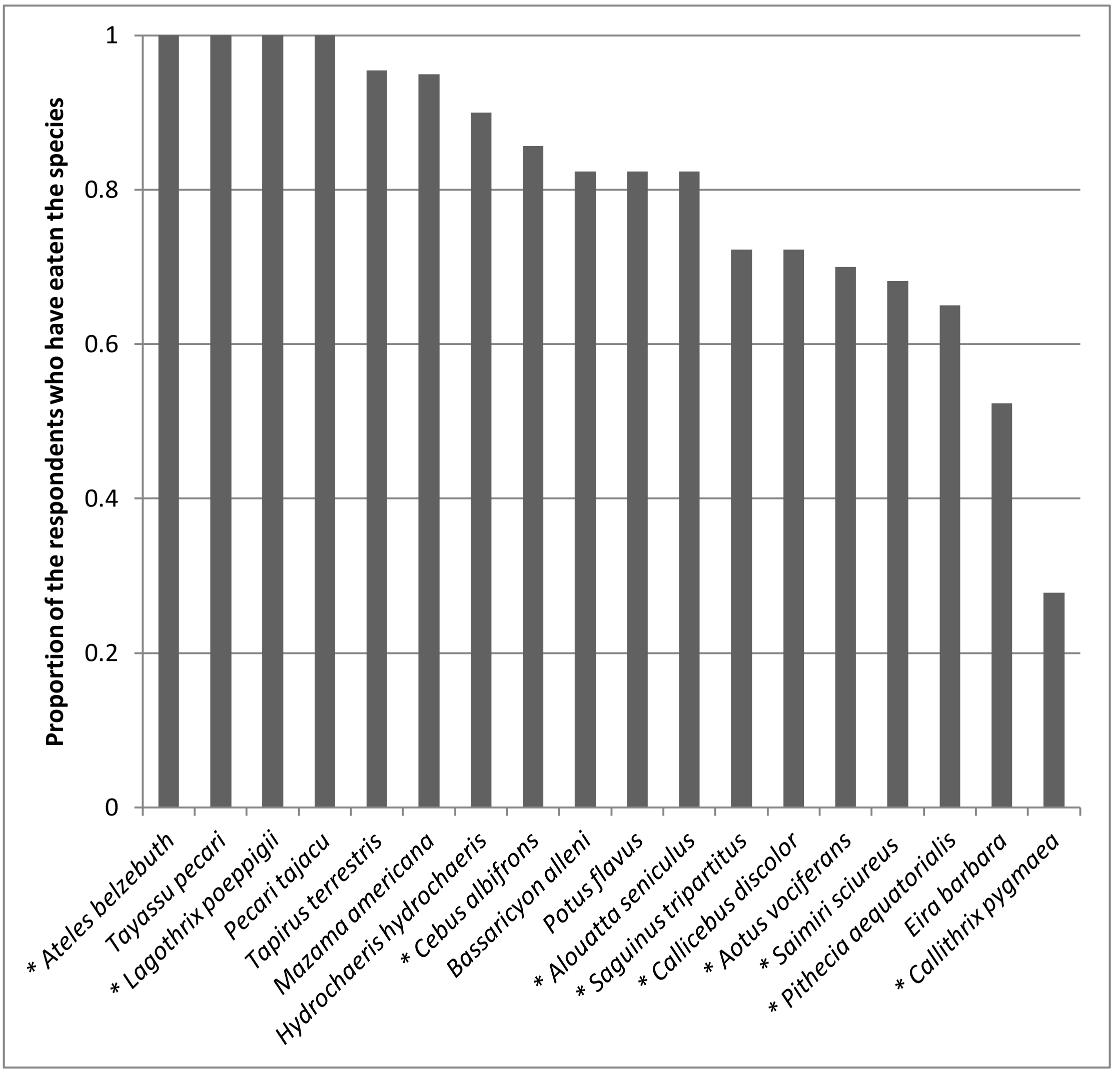

Figure 3.9. Proportion of participants who recognised each of the 18 focal species who reported eating it. Sample size varies between 23 and 17 participants. Primate species are indicated with an asterisk (*).

Various taboos were mentioned during conversations with individuals, although most were personal or temporal, rather than prescriptive. Both spider monkeys and saki monkeys were mentioned as species which should not be eaten by pregnant women, with one individual stating that the child will be thin if this happens. Saki monkeys were said to make people ill, as were spider monkeys and the tayra, which gave some individuals headaches and made them feel dizzy. Capuchin monkeys made some individuals tremble. Other individuals also stated they did not like howler monkey, as they had a lot of worms in the meat and tasted bad, but others mentioned howler monkeys as one of their favourite meats, suggesting that this was a preference, rather than a taboo.

Cultural salience

Woolly monkeys were the most frequently named species during free listing, and also had the highest salience of any species (Figure 3.10). However, the frequency with which individuals

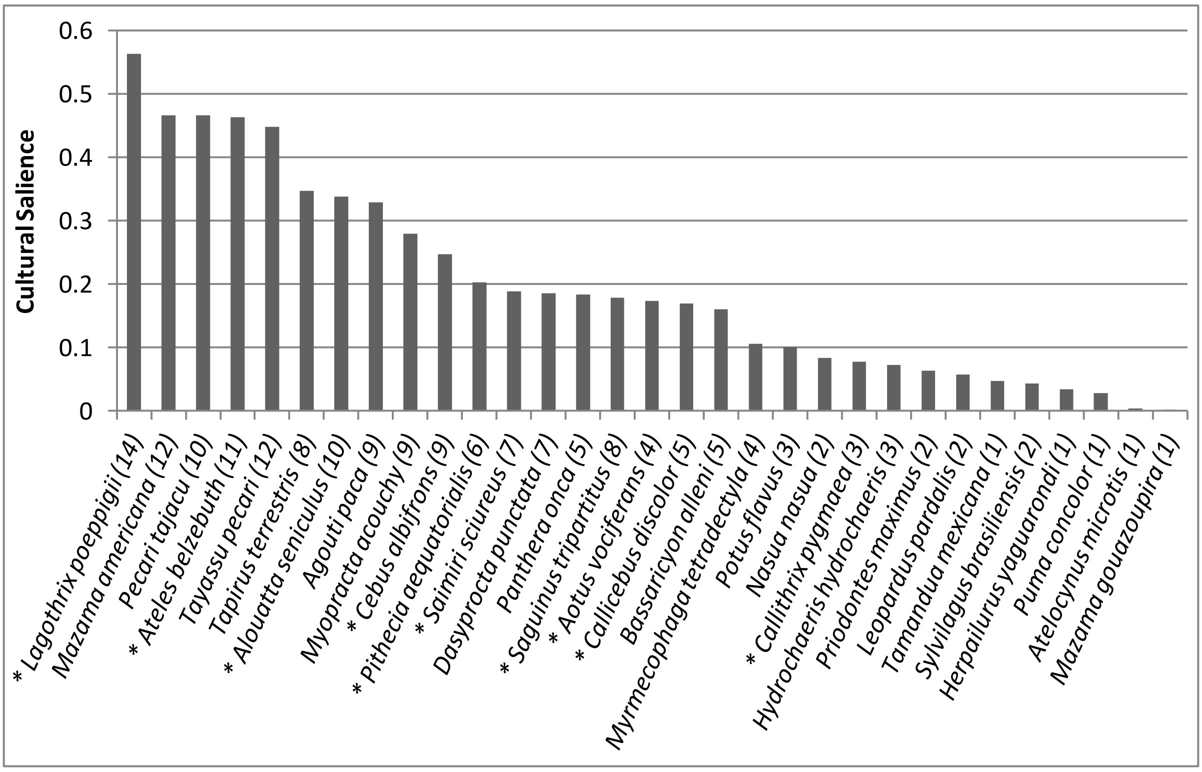

Figure 3.10. Cultural salience of all mammal species named during free lists by 18 individuals. Primate species are indicated with an asterisk (*). Number of participants who named each species is shown in brackets after the species name.

named primates, and the mean average position of primates in individuals' lists was almost identical to that of all other mammals, and the mean cultural salience of primates was slightly lower (rank ranges between 1 and 31. Salience ranges between 0 and 1. Primates: frequency = 88.9%, mean rank = 7.88, salience = 0.515. non-primates: frequency = 88.9%, mean rank = 7.69, salience = 0.575).

Factors associated with species of high cultural salience

Many species which were included in the dataset had no contribution to the diet as reported by Franzen (2006). However, the single variable which best explained the cultural salience of species was dietary contribution (Table 3.3). Cultural salience increased as species gave a greater contribution to the diet (linear model, n=31, $F_{1|29}$= 84.9, p<0.001, adjusted R^2 = 0.74, Figure 3.11). The second best model had almost equal weight as the best model, and although this model indicated that traded species had higher cultural salience, this difference was not significant (p=0.127). There was little support for the hypothesis that primates had greater cultural salience than other species, once contribution to the diet had been accounted for.

Table 3.3. Factors explaining cultural salience of 31 mammal species for the Waorani. Models where ΔAICc<4 are shown, all models are displayed in Appendix 2. IND = Log number of individuals in diet

Model	**AICc**	**ΔAICc**	**Model weight**
IND	-62.57	0.00	0.32
IND + Trade spp (Y/N)	-62.55	0.02	0.31
IND + Trade spp (Y/N) + interaction	-61.00	1.57	0.15
IND + Trade spp (Y/N) + primate spp (Y/N)	-60.62	1.96	0.12
IND + primate spp (Y/N)	-60.32	2.25	0.10

Variable importance: IND = 1.00; Trade = 0.58; Primate = 0.22; IND x Trade = 0.15

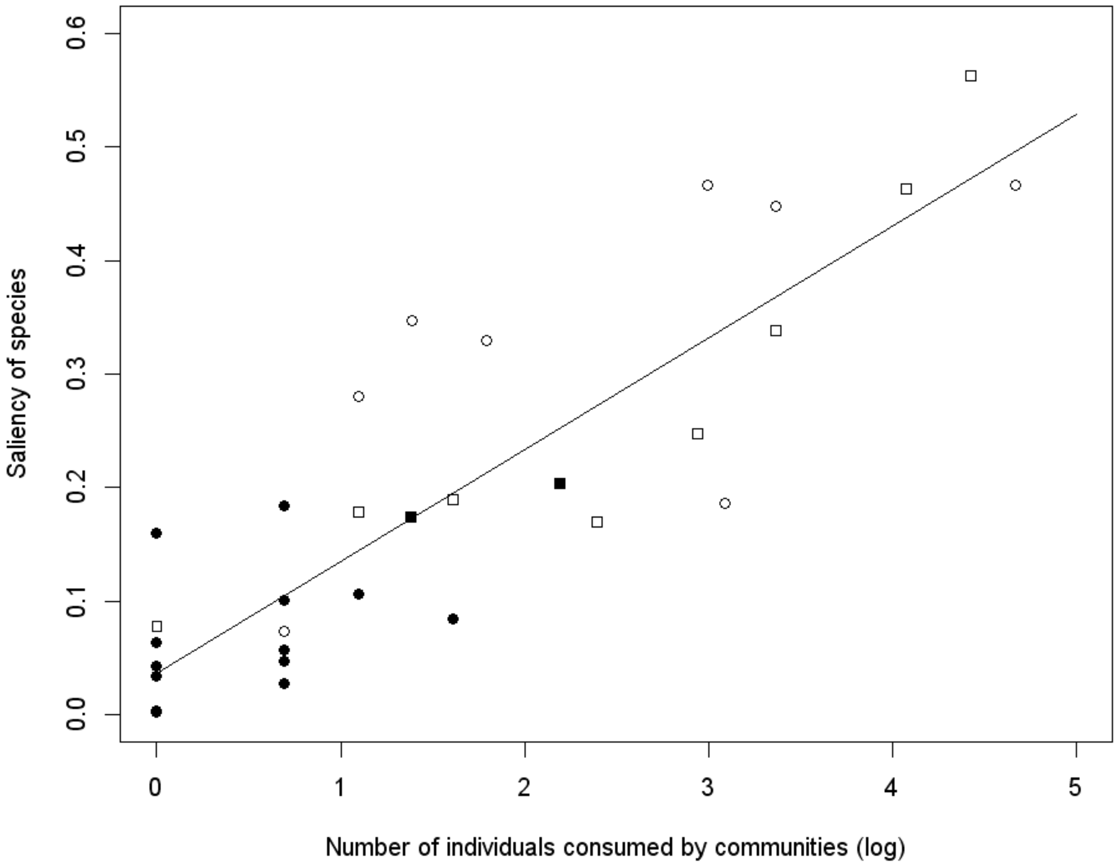

Figure 3.11. The relationship between cultural salience and dietary contribution of 31 species. Primates are square, non-primate species are open circles. Traded species have open symbols, non-traded species have filled symbols.

3.4. DISCUSSION

Previous research has emphasised the cultural importance of primates in traditional Waorani society (e.g. Rival, 1993). Given the extensive changes in Waorani society in the 50 years since first western contact, the results of this study should not be interpreted as representing traditional Waorani perceptions of primates and other animals, but rather as observations on the contemporary ethnobiology of the Waorani.

3.4.1. Primates as a distinct group

All primate species were identified as *monos* by informants and primates were generally more frequently grouped with other primates during the pile sorting exercise. However, the kinkajou and olingo were also referred as *monos*, specifically *monos nocturnos*, and were placed together in a group with the night monkey by a number of informants during the pile sorting exercise. Informants explained this grouping because all three were nocturnal, and lived in the same way; you could find them during the day by banging on hollow trees. This grouping of a primate together with kinkajou and olingo is consistent with naming systems in other parts of the lowland neotropics, where the kinkajou and olingo are referred to as monkeys (e.g. Lizarralde, 2002; Urbani, 2006). Tayra were also grouped with primate species a number of times. Tayra were seen as a species which transcended the groups of animals “arriba” and “abajo”, as it spent time both on the ground and in the trees, but it was recognised by informants as being different from monkeys as it had “paws”. Other pawed arboreal animals, such as the squirrel, were also never referred to as monkeys. Therefore the grouping of kinkajou and olingo with primates appears in part to be because of their shared space use in the trees, shared nocturnal behaviour, and use of tree holes as sleeping sites like the night monkey, and because they, like monkeys, have hands rather than paws. This perception of *monos* as a group which includes the kinkajou and olingo may be a consistent pattern of folk taxonomy across the Spanish speaking lowland neotropics. Folk taxonomy in Amazonia may be an area for further study, as a clear understanding of how people categorise the animals in their local area can inform conservation. Researchers and conservation practitioners should take particular care that both they and those in the studied culture are referring to the same group of animals with this term, particularly when planning a project with primates.

3.4.2. Consumption and dietary overlap

Mammal species which all participants reported they had eaten in this study were also the most consumed species based on five months of data collected by Franzen (2006). However, this study also identified three species not previously recorded as consumed by the Waorani (Mena V et al. 2000; Franzen 2006). The tayra was not named in any free list, nor has it previously been recorded in Waorani diets, but in this study it was perceived as the biggest crop-raider, and had been eaten by about half of the informants. Tayra may have not featured in previously studies of Waorani wildmeat, as although tayra are eaten, they are not hunted but usually killed as crop raiders, and thus informants may not have reported this, perhaps as the meat was not brought back by “hunters”. Tayra, olingo and the pygmy marmoset have not previously been recorded in studies of Waorani diets (Mena V et al. 2000; Franzen and Eaves 2007). These results support the assertions of Rist et al. (2010) that LEK is useful for rapid evaluation, and validating rare results. Although these three species may not be frequently eaten, they had been consumed by numerous participants in this study, and this dataset was collected in a fraction of the time taken to record consumption in previous studies.

Although the Waorani are reported to have over 409 names for plants used by animals, and only 150 for plants used as food for humans (Rival 2009), the wild plants most frequently named as animal food in this study were also those most consumed by the Waorani. Furthermore, for all but two species, participants most often named food items consumed by the Waorani when asked to name food items consumed by focal species. This suggests that either the Waorani have an anthropocentric perspective of consumption by the focal species, or the focal species chosen by the researcher consumed the same species as the Waorani. A closer investigation of four primate species for which western scientific data were available provided greater support for the hypothesis that Waorani had an anthropocentric view of animal diets than the hypothesis that focal species consumed the same as the Waorani. Nine of ten plant species perceived to be consumed by these primate species were also consumed by the Waorani in this study, but plant species important to the spider monkey, and also perceived as edible by Waorani (Mendoza Troya 1994) were not mentioned. The species named by the Waorani as being consumed by spider monkeys have been reported in the scientific literature to contribute a combined total of less than 2% of spider monkey diets

(Suarez 2006). In contrast, *Naucleopisis ulei*, contributing 4.7% of spider monkey diet in Suarez's study, and the second most consumed species, was not mentioned by respondents, even though the Waorani have a name, *awenkatumo*, for this species (Mendoza Troya 1994).However, that does not mean that their assertions were incorrect. Participants correctly identified some plants which were eaten by the spider monkey, and those species which they identified for which there is no record of spider monkey consumption may have been less eaten or available for the specific groups which were studied by Dew (2005) and Suarez (2006).

3.4.3. Cultural importance of primates

Rival (1996) suggests that the Waorani are not interested in peccary species, and never sought to hunt them. In contrast, she states that the Waorani considered monkeys more interesting; monkeys frequently featured in traditional stories, and men retold stories of hunting trips which encountered monkeys. Woolly monkeys were the preferred primate for consumption, and are also the most consumed primate by the Waorani (Franzen, 2006, 42% meat weight of primates; Mena V et al., 2000, 22% meat weight of all species).Nevertheless, although woolly monkeys were clearly important to the Waorani, as they were named by most individuals during free listing and had the highest cultural salience of any species, there was no evidence which suggested that primates as a group were more important than other mammal species. On average primates had lower salience than other species, and the best predictor of cultural salience was dietary contribution, rather than species group. In general, cultural importance for the Waorani is better described at the species, rather than order level. Two species recurrently appeared important: the woolly monkey and white lipped peccary. These two species contribute the greatest number of individuals to Waorani harvest of mammals in the area (Franzen, 2006), were highly recognised by participants, had high cultural salience and were preferred species for consumption. Although other primate species make important dietary contributions, have high salience and were also named as preferred species (e.g. the spider monkey), these characteristics could not be generalised to all primates. During the study period, households had numerous pet monkeys of various species, but particularly woolly monkeys. However, these pets did not have their own miniature houses, as reported by Mondragon & Smith (1997), but usually lived either inside the house or outside attached to a string. Breast-feeding of these monkeys was neither observed nor reported – most individuals reported feeding their pets cultivated fruits and chicha, a mildly alcoholic drink usually made primarily from yuca.

Interestingly, although numerous wild animals were reported to eat domesticated crops, no domesticated animals were named during free lists. Some households owned chickens, and most households had one or more hunting dogs, but these domesticated species are recent additions to Waorani fauna, being introduced since first western contact a little over 50 years ago. This has implications for conservation, as projects which incorporate species with high cultural salience may be more successful than those working with less salient species. More salient species are likely to be perceived as more important in local communities and local knowledge of these species may be higher. For the Waorani, this suggests that projects promoting domesticated species as protein alternatives for wildmeat may be unlikely to succeed, whereas projects based on high salience species such as the woolly monkey and white-lipped peccary may have higher resonance in the communities. Furthermore, if the pattern found in this study of increased salience of more consumed species is found in other communities, focusing conservation projects on species with high salience is also likely to focus projects on species which are important to local diets and may be more prone to over-exploitation. On the other hand, focusing conservation projects on these important species may also lead to conflicts if a reduction in consumption of these species is promoted.

3.4.4. Methodological insights

Ethnoprimatological studies assert, by their nature, that primates are particularly worthy subjects of research in the studied culture, but these assertions need to be critically examined. By focusing on primates, ethnoprimatologists may overlook other species whose interactions with humans may be important for the conservation of an entire ecosystem. For example, the available evidence suggests peccary species may supersede the importance of primates in the diet of many Amazonian peoples. Although large bodied monkeys and peccaries recurrently feature in the diet of people which rely on wildmeat as a source of protein, many have demonstrated that peccary species are the most important species for human consumption (e.g. Franzen, 2006; Parathian & Maldonado, 2010; also in a review of several studies by Sponsel, 1997). As one of the ultimate aims of ethnoprimatology is to inform conservation, a broader focus on the place of primates in the ethnobiology of a community can only be of benefit. Ethnoprimatologists should take care to place primates within this context before embarking on studies focused particularly on primates. Without these precautions, ethnoprimatology risks imposing western taxonomic groups on indigenous peoples, rather than allowing them to define themselves which species are more important. In focusing on the wider fauna in a study area, at least during the initial stages of a project, these dangers can be avoided.

Although most focal species were consistently identified by participants, many had trouble identifying species from photos, particularly the similar olingo and kinkajou, which informants largely distinguished on their size and calls. Although the implications of this confusion were not serious in the current study, multimedia prompts, such as video, or combinations of photos and call playbacks would have improved identification of these species. This observation has particular implications for projects which use photographic methods to elicit LEK in order to identify the presence of specific species. For example, Dechner (2011) used visual prompts to enable local informants to identify forest fragments where the black mantled howler monkey (*Alouatta pallinata*) had been observed. Although 38% of individuals recognised *Alouatta pallinata*, howler monkeys are very cryptic species, and vocal encounters are more frequent than sightings (personal observation). Call playbacks may have increased individual recognition, and identified more areas where the monkeys were present. In a further complication, similar-looking *Alouatta seniculus* also occurred in the study area, and individuals may have confused the two species, or may not view the two as separate species. When attempting to gain information about one particular species using these methods, conservation practitioners should consider including similar sympatric species, to ensure that informants identify the focal species as a distinct animal type, and to ensure that both the practitioner and informant are discussing the same species.

Some species may contribute little to the diet of a community, have little dietary overlap or be rarely seen, yet still be considered culturally important. An example of this type of species for the Waorani is the jaguar – rarely seen or eaten, but nevertheless culturally significant (Rival, 2002). Measuring the importance of species to specific cultures needs to include not only dietary measures, but also factors such as presence and prevalence in local mythology, religion, language and medicine. Free listing and cultural salience is one method to try and capture this complex variety of ways in which species can be considered important by individuals (Riley 2006). Having said this, in this study, cultural salience of species was best predicted by the contribution of the species to the diet of the Waorani, and jaguars were mentioned by only five participants. However harvest levels are not independent of environmental carrying capacity and historical hunting in an area, and changes in cultural salience may lag behind environmental dynamics. For example, in areas where overharvesting is significant and preferred species are locally extirpated, similar analyses could suggest these extirpated species are more culturally salient than expected by their contribution to diet. The impact of historical versus current consumption on cultural salience is an area for potential future investigation.

3.4.5. LEK and ethnocentricism

The validation of LEK against information collected within a western scientific framework is criticised as devaluing LEK (Brook and Mclachlan 2005), and criticism of LEK often taken as criticism of the culture from which it originates and thus the criticism is condoned as ethnocentric (Nelson 2005). Comparisons of western scientific knowledge and LEK are always conducted from the perspective of the western scientist, often with the implicit and unvoiced assumption that there exists some objective truth which can be identified by congruence in the observations of LEK and scientific knowledge (Rist et al., 2010). However, these comparisons remove LEK from its cultural context and assume that the information gathered is acultural and objective (Nelson 2005). However, LEK is neither objective nor acultural – by its very definition LEK is subjective and culture specific. In this study, human consumption of plants correlated with perceived diets of focal animal species, and the cultural salience of mammals was found to correlate with human consumption of these species. These observations suggest the Waorani view their natural environment through the context of their own culture. This ethnocentric perspective is widely acknowledged in anthropology and is present in all cultural systems, including western scientific culture, but rarely acknowledged in conservation or LEK studies (Nelson 2005). This ethnocentricity should not be viewed as "invalidating" LEK; which, collected with the aim of understanding the perceptions and knowledge of the environment by a particular culture, is intrinsically valid and non-falsifiable.

This perspective has implications for those who wish to use LEK for conservation and natural resource management. In these contexts, LEK has largely been used to suggest alternate management practices, or as an alternate or complementary information source for western scientific knowledge. Acknowledging the ethnocentricity of LEK does not invalid the knowledge contained, but rather serves as a reminder that such information should be viewed within the context of an entire culture. Comparisons between western scientific knowledge and LEK are valid, not as an attempt to validate LEK, but as a process in which observers may understand the congruence and incongruence between his or her own knowledge and that of others. This process is perhaps best conducted as a mutual exercise designed to exchange knowledge from the perspectives of local people and outside observers, with both approaching the exercise with the point of view that the other may be right.

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Chapter 4

Movement ecology of human resource users: Using net squared displacement, biased random bridges and resource utilisation functions to quantify hunter and gatherer behaviour

4.1. INTRODUCTION

The study of how animals and plants move from one place to another, or movement ecology, is a growing field, which recognises the contribution of internal states like hunger, and external factors such as resource distribution, to animal movement. Habitat selection research examines how organisms use their environment, by focusing on identifying features associated with use of an area. In spite of overlapping areas of interest, integration of movement ecology and habitat selection has been slow (Holyoak et al, 2008), partly hampered by differences in data treatments and requirements, and the lack of a methodological framework to tackle these differences (Cagnacci et al, 2010; Holyoak et al, 2008; Calenge et al. 2009). Incorporating the two disciplines can move movement ecology past a purely mechanistic understanding, and aid more accurate assessment of habitat selection. A combined approach would benefit both ecological studies of non-human animals and studies in conservation.

Conservation science frequently uses models of human behaviour to investigate hunting and sustainable resource use (e.g. Rowcliffe et al. 2003), but outside a small number of studies on recreational hunters in temperate zones (e.g. Lange et al, 2010; Kaltenborn and Anderson, 2009), human hunter movement and habitat selection have not been quantified. Humans are central place foragers: they extract resources from an area around a central place, usually a community (Houston, 2011). Research on the sustainability of wildmeat hunting frequently uses estimates of the area of resource extraction in order to calculate sustainability indices (i.e. Hill and Padwe, 2000; Levi et al, 2009). These studies usually use the furthest distance travelled by members of the community and assume a uniform circular area of extraction around a community, or assume that use is most intense in areas closest to the community, but this is rarely demonstrated through empirical research. Accurate assessment of areas of extraction and habitat preferences will improve these estimations, and aid prediction of areas individuals use outside a specific study area. Source-sink dynamics is another commonly used theory in conservation science (i.e. Hill and Padwe, 2000), which assumes that unexploited areas can act as sources of new individuals for exploited, or sink, areas. Accurate estimation of exactly which areas are used and unused by humans, coupled with ecological information such as dispersal distance of exploited species, would help estimate the relevance of source areas to the dynamics of different exploited species.

Detailed information about an individual's location can most easily be gained through GPS tracking (Cagnacci et al, 2010), which records an individual's location at set intervals. Whereas gaining location data for animals involves stressful, potentially dangerous and expensive trapping and tagging, humans can be asked to carry small inexpensive GPS receivers which record locations. Given the ease with which GPS information can be gathered for humans, the development of appropriate methodology is crucial, particularly as some characteristics of human movement ecology mean that traditional habitat selection methods are harder to apply. Firstly, humans are often central place foragers – they collect resources in a single day, starting from and returning to a community. Secondly, like some other animals, humans often repeatedly use the same paths, for instance along ridges or cuttings through dense forests. Finally, when hunting, humans are like many other predators and so should select for prey presence rather than specific landscape features. As human hunters usually hunt a wide spectrum of prey animals, there are less likely to be specific landscape features associated with the various target species than there are for more specialist predators.

4.2. METHODOLOGICAL FRAMEWORK

We present a combination of three methods to integrate movement ecology and habitat selection for GPS track data. Although this methodology was developed to overcome issues specific to data collected from human hunters, the framework is applicable to other study species which use central places. Resource extraction of central place foragers is made up of three components: the outward journey, a period of resource extraction and the return journey (Orians and Pearson, 1979). Central places are points to which an individual returns on a regular basis. This includes many species, such as fish returning annually to spawning grounds, human hunters returning daily to their community, or diving mammals who return to the surface to breathe. We propose using net squared displacement (NSD) combined with non-linear mixed models to estimate the distance travelled and the area of resource extraction. Biased random bridges (BRB) are then used to define utilization distributions (UD), and resource utilization functions (RUF) identify habitat features associated with greater use (Figure 4.1). The combination of these methods creates a flexible framework which can overcome issues associated with integrating movement ecology and habitat selection.

4.2.1. Distance, duration and speed: Net squared displacement (NSD)

NSD calculates the squared distance between each GPS location in an individual's track and the individual's original location. Distances are squared to remove directional information. NSD has previously been used to study yearly movement cycles of migratory and dispersing animals (Bunnefeld et al, 2011; Börger and Fryxell, in press). Although its appropriateness at smaller temporal and spatial scales has not been demonstrated, the approach is scale-independent and we test here its applicability to tackle ecological questions of habitat selection during different movement states. Plotting the NSD over time gives a curve starting at zero when an animal is at the central place, with NSD increasing until it reaches a maximum location. NSD can then remain relatively constant until the animal starts to return to the central place, when NSD will gradually decrease until the animal reaches the central place, where NSD = 0 (Figure 4.2). From modelling NSD, key parameters such as distance travelled, duration and speed can be mathematically defined. Single trips can be compared with the population mean, or comparisons made between different individuals or classes of individual within a population. If animals make multiple trips to and from the central place in a single day, such as birds caring for young in a nest or defending key central resources such as mating display areas, each trip in the day can be modelled

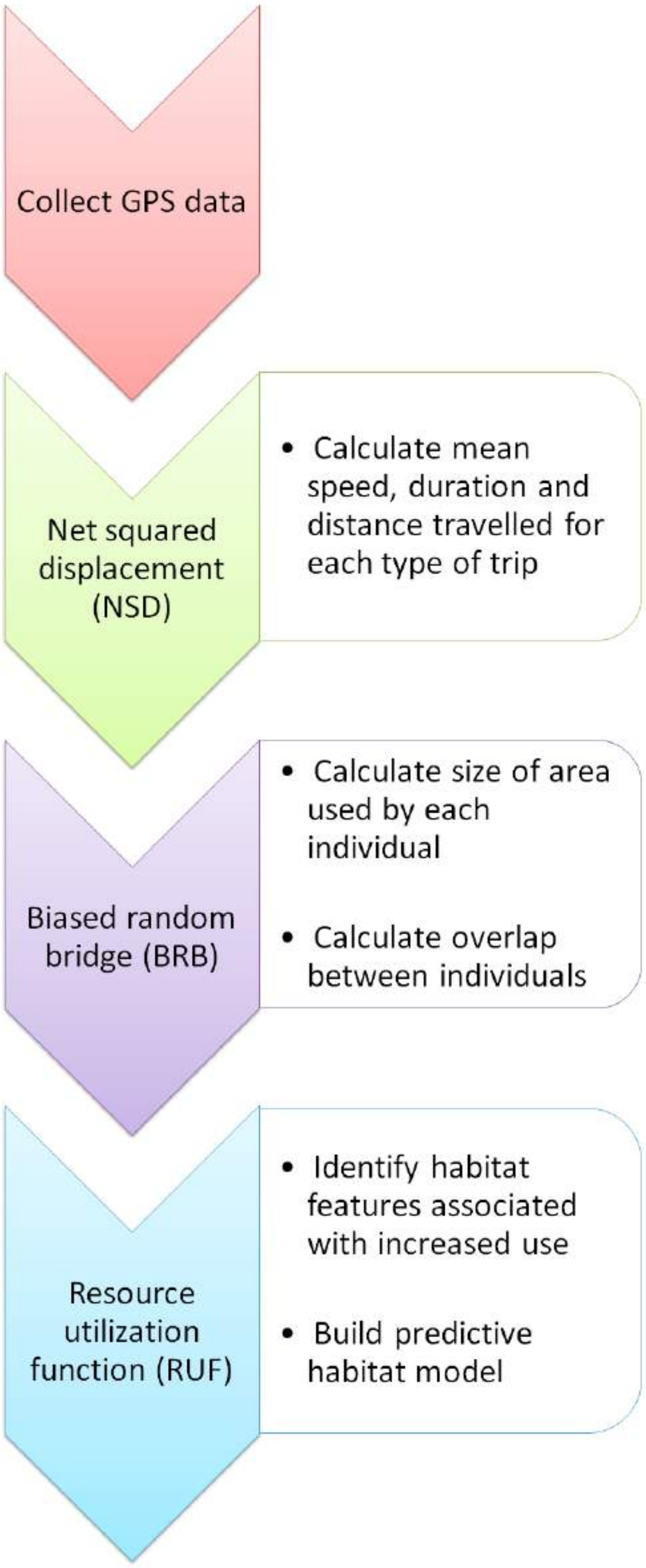

Figure 4.1. Methodological framework outline and potential outcomes of each step

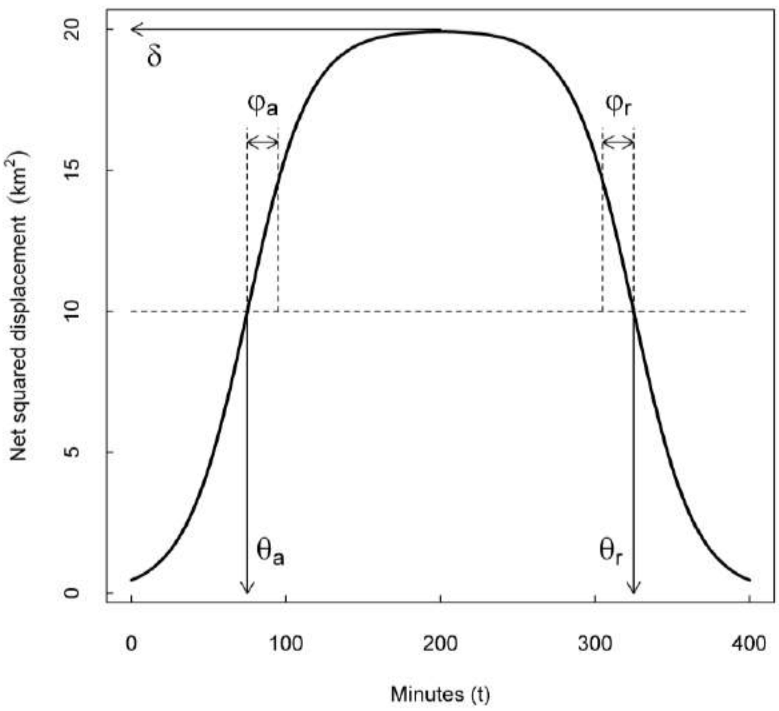

Figure 4.2. Measures used when modelling NSD using eqn 4.1. δ = asymptotic height, θ_a*= time when half the asymptotic height is reached on the outward journey,* θ_r *= time when half the asymptotic height is reached on the return journey* φ_a *= time taken to travel between half and approximately three-quarters of the asymptotic height on the outward journey,* φ_r *= time taken to travel between half and approximately three-quarters of the asymptotic height on the return journey. For this figure, δ = 20,* θ_a*=75,* θ_r *=325,* φ_a *= 20,* φ_r *= 20.*

separately. A double logistic function (eqn 1.) can be used to model trips, as outlined in Bunnefeld et al (2011).

$$NSD = \frac{\delta}{1+\exp\left(\frac{\theta_a - t}{\varphi_a}\right)} + \frac{-\delta}{1+\exp\left(\frac{\theta_r - t}{\varphi_r}\right)} \qquad \text{eqn 1.}$$

Where δ is the asymptotic height of the distance travelled from the community, θ_a and θ_r are the times at which half the asymptotic height is reached on the away and return journeys respectively. φ_a and φ_r model the time between reaching one half and $\frac{1}{1+e^{-1}} \cong \frac{3}{4}$ of the trip on the away and return journeys, and thus define trip duration (Figure 4.2). Number of minutes since the trip started is represented by t. Different parameters for the away and return journeys allow the timing and speed of travel to differ on the two elements of the trip (Figure 4.3).

Representative speeds of away and return journeys can be calculated using one quarter of the asymptotic height divided between the time taken to travel between one half and three quarters of the trip : $\frac{0.25\delta}{\varphi}$. By modelling NSD with non-linear models, the parts of the journey can be mathematically defined and separated for analysis. The part of the journey which is separated for analysis will depend on the study system and specific research questions. For example, in animals which use central places, such as nests or dens, only an outward journey may be of interest as the return journey is a function of central place location. In human hunters, hunting is more likely to occur on the outward journey, as hunters return to their community once successful. Thus the outward journey is a searching phase, as hunters search for an animal they can successfully kill, followed by resource extraction. In contrast, the return journey (though likely similar to the outward journey) will be of less interest. This assumption may not be true in areas with low prey densities where hunters may also hunt on the return journey if unsuccessful (e.g. Alvard, 1993), but should be established for each study site. An additional issue for species which use central places is that analysis of raw data would produce a strong preference for the habitat type where the central place is located (Benhamou, 2011).

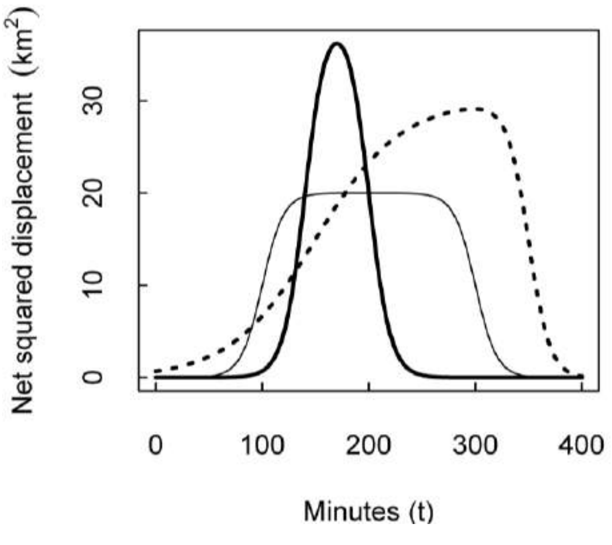

Figure 4.3. Three definitions of NSD using a double logistic model, demonstrating the flexibility of non-linear models. Solid line: δ = 40, θ_a= 140, θ_r = 200, φ_a = 10, φ_r = 10. Dotted line δ = 30,θ_a = 150, θ_r = 350, φ_a = 40, φ_r = 10. Dashed line δ = 20, θ_a=100, θ_r = 300, φ_a = 10, φ_r = 10.

An important contribution of movement ecology to habitat selection would be the identification and separation of travelling and non-travelling periods (Börger et al. 2008), and this can be achieved by modelling NSD. Non-travelling periods are often equated with foraging or feeding periods, and can normally only be separated from travelling periods when time between recorded locations is expected to be shorter than the non-travelling periods. Most studies using GPS tracks use the relationship of distance travelled between recorded locations (step-length) and relative angle between three consecutive locations (turning angle) to distinguish behavioural changes in individuals movement (Gurarie et al. 2009). Individuals are assumed to be foraging when step lengths are shorter, and turning angles more tortuous, and travelling when turning angles are less tortuous and step-lengths are longer. Cut-off values for separating the step-lengths and turning angles into travelling and non-travelling periods can be determined through statistical exploration of the data (Gurarie et al. 2009), but if GPS location error is greater than the cut-off length, non-travelling periods could be incorrectly classified as travelling periods (Frair et al, 2010). Therefore these methods are only appropriate in animals where non-travelling periods are longer than recorded location intervals, and travelling between location intervals is expected to be greater than location error. This greatly reduces the species for which this method can be applied. In contrast, when modelling NSD with non-linear models, it is not necessary to define cut-off points for step-length and turning angle, but travelling and non-travelling periods can be identified, mathematically defined and separated. Furthermore, non-linear models of NSD can extrapolate between recorded locations, and so are robust to missing locations, a frequent problem in GPS tagging studies. Finally, these models can be applied to a wide variety of species, ecological questions and various location intervals.

If the area of resource extraction is assumed to be represented by the peak area of the curve because hunters return to the community once they are successful (Figure 4.2), it too can be simply identified and isolated. The peak area is not identical to the asymptotic height δ, which, by definition, is never reached, but can be derived from the parameter estimates of the non-linear mixed model. The extent to which δ approximates the peak of the curve should be checked, and the difference may be significant in some situations. In these cases, and when other properties of the double logistic function are unlikely to be appropriate (such as gradual acceleration and deceleration close to the central attractor) alternatives to the double logistic function (for example, double asymptotic functions) should be explored, though the methodological framework remains valid.

4.2.2. Area, intensity of use and selection of landscape features: Biased random bridge utilization distributions (BRB) and resource utilization functions (RUF)

Multiple locations of a single individual recorded by GPS units are non-independent, as the location of the next position in the sequence at any time-scale is bound by the animals' potential for movement within the given period. Locations are also non-independent as nearby locations are often more similar to one another than more distant locations (Boyce et al, 2010). Both of these factors mean that data are autocorrelated, which is a problem for studies based on parametric statistics. One method to reduce autocorrelation is data thinning (Swihart and Slade, 1985), but this can remove real patterns of animal behaviour, particularly in resource selection studies. For example, an animal will show high autocorrelation if locations are recorded every 10 minutes, and they "select" to stay in the same area (the definition of "same area" also varying with spatial scale and normal daily geographical extent of animal) for an hour (Figure 4.4). If

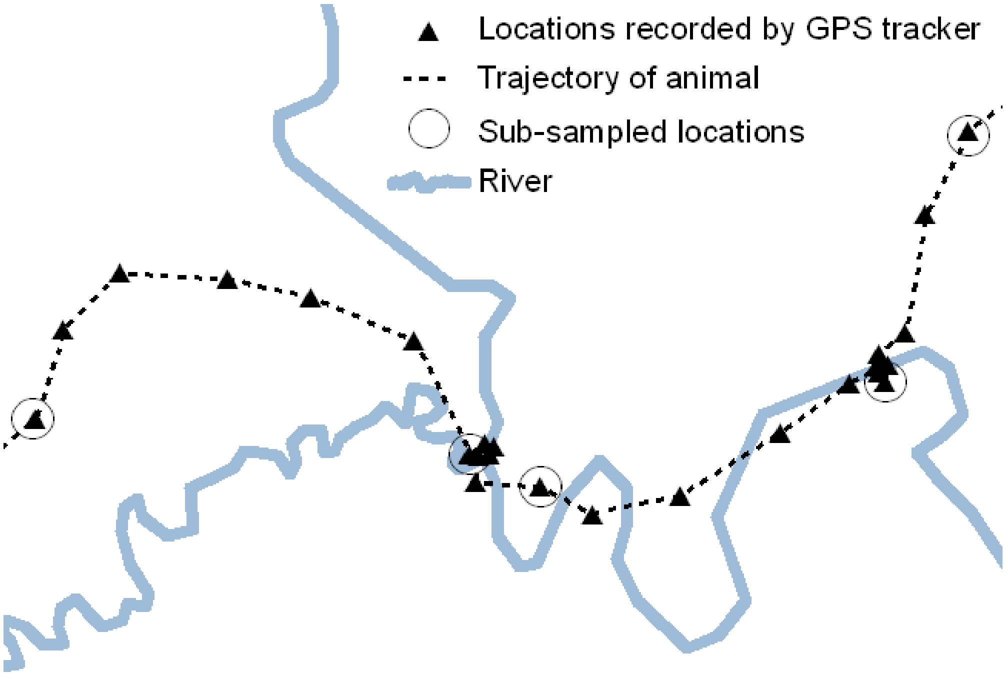

Figure 4.4. Example animal trajectory, showing strong selection of riverside areas in the raw data, and the potential loss of this relationship when locations are sub-sampled (circled locations).

data are thinned to one point every hour (circled locations, Figure 4.4) to reduce autocorrelation, the selection of this area is lost in analyses. Data thinning also occurs when methods require locations to be recorded at equal time intervals. Missing locations are common in GPS tracks, due to landscape features blocking satellite signals (DeCesare et al. 2005), and these missing locations mean unequal intervals between locations. In these cases, biologically important information is lost in order to make data conform to the assumptions of habitat use methods. The proposed methodological framework does not require data thinning to remove autocorrelation, and can interpolate missing location from recorded locations.

Choice of statistics in resource and habitat use studies has been discussed in numerous review papers (e.g. Johnson et al, 2006; Thomas and Taylor, 2006; Millspaugh et al, 2006; Conner et al. 2003). Most approaches compare characteristics of locations where a species is observed to be present to characteristics of absent or available locations in a study area. Comparisons between observed and available locations are considered more robust due to difficulties in identifying absent locations (Johnson et al, 2006). Other authors (Thomas and Taylor, 2006) have argued that available locations are also difficult to identify, due to uncertainty about the accessibility of locations to a species, and temporal differences in environmental variables such as vegetation cover. For both these types of study, categorical characteristics such as “heathland” are assigned to each location. Locations can, however, be misclassified if GPS location error is great (Frair et al 2010). Conner et al. (2003) found that categories were less able to identify the importance of edge habitats when compared to distance based analyses where a continuous measure of distance to each habitat feature of interest is calculated for each location. Nevertheless, using continuous variables creates new problems. If a species is selecting a particular habitat type, observed locations should show smaller variance in distance to this habitat than for all available locations, making it difficult to use parametric analyses (which require homogeneity of variance across conditions). For example, human hunters frequently follow paths through the forest, but will sometimes leave paths to pursue animals or explore new areas. Areas away from paths should be considered as available habitat as they are sometimes, though less frequently, used. If random locations are generated in this landscape to represent the available landscape, a much higher variance in distance to path would be expected for these locations than observed hunter locations. Equal variance in this case would a priori lead to the conclusion that hunters are not selecting for paths, thus making testing redundant.

Resource utilization functions (RUF) can be used to examine resource use by relating landscape features to a probability distribution of an individual or species use of the landscape. These probabilities, or utilization distributions (UD), are frequently used in movement ecology, but are not often linked to landscape features or used for habitat selection studies. Using UDs, area of use and overlap between individuals or types of individuals can be calculated. Kernel methods smooth observed locations of a species or individual to create an average probability of use for each square in a gridded area. This probability of use for each grid square is then converted to a value between 0 and 100 in which lower value grid squares are more intensively used. Bridging kernel methods are considered an improvement on traditional kernel methods (Benhamou and Cornélis, 2010), as they place a kernel function between successive locations rather than over known locations. This means that the area used to move between points is considered and all observed locations of an individual are connected. Traditional kernel methods could leave disconnected use areas in home range estimates of terrestrial animals, which is not ecologically realistic, as it must be assumed that individuals use corridors linking areas. Kernel bridges can also bridge gaps where locations are missing (Benhamou, 2011). In the biased random bridge (BRB) method, movement is biased towards the next location, an improvement over existing kernel bridging methods which use random movement to model this process (Calenge, 2011). An additional advantage of BRB is its ability to incorporate natural boundaries into the calculation of UD, such as constraining estimations so that terrestrial animals never use lakes. Furthermore, the smoothing factor for BRB, a significant source of error in kernel studies (Millspaugh et al, 2006) can be automatically estimated from the data. Using BRB to interpolate between known locations means that missing locations are estimated from the data and thinning of the GPS data is not required.

RUFs assume that increased height of the UD in a grid square represents selection, and uses multiple regression to relate use intensity of all the grid squares in the study area to landscape features, such as distance to a river. The probability of use for each grid square is subtracted from 100 to give a log-normal distribution. Thus if grid squares closer to the river are more intensively used, then the RUF will output this as a positive coefficient estimate. As the use intensity and landscape features of any grid square will be correlated with that of adjacent squares, a Matern correlation function is used to account for the spatial correlation of the grid cells (Marzluff et al, 2004). The Matern correlation function has two parameters 1) ρ, the range of spatial dependence in metres, and 2) θ, the smoothness of the UD surface. This method can be used to compare habitat selection between different individuals, compare the relative importance of various environmental variables in explaining use intensity, and develop predictive models of species distribution. Although continuous variables should be normally distributed to be included in an RUF, non-normal variables can be transformed and or changed to categorical variables (Marzluff et al, 2004). RUFs can only identify increased or decreased use associated with features within a researcher defined study area, but as analysis is based only on observed locations there are reduced errors from generating random locations. As it is not necessary to generate random or unused location for analysis, uncertainty about whether areas are truly unused or random is removed, and it is not necessary to ensure equal variance between the two sets of locations.

The outlined methodological framework, combining NSD, BRB and RUF methods, is flexible and can be applied to track data to address various questions of ecology, conservation and human behaviour. Each step uses the most biologically realistic methods available, and this three-step combination can account for missing locations and spatiotemporal autocorrelation (Table 4.1). Additional information on the application of all three methods can be found in Appendix 3. Below, I demonstrate the use of this framework by using GPS tracking data to determine if movement ecology and habitat selection differs between hunters and non-hunter.

4.3. METHODS AND MATERIALS

4.3.1. Data collection

Data on movement during forest trips was collected from 12 individuals in a small Waorani community inside Yasuní National Park, Amazonian Ecuador (0°41’S latitude, 76°24’W longitude) which with the adjacent Waorani Reserve covers 1.6 million hectares. Ridges of 25- 40m are

Table 4.1: Strengths, limitations and assumptions of combined methodology using net squared displacement, biased random bridges and resource utilizations functions.

Strengths	**Limitations**	**Assumptions**
Methods are biologically meaningful and give uncertainty associated with parameter estimations	All three methods require large numbers of locations	Species movement highly influenced by central places
Can be applied to GPS tracks of any collection frequency and spatial scale that is expected to detect an individual's relocation	Not able to identify multiple resource use areas in a single trip	Sampling frequency more frequent than duration of resource extraction bouts
Can be applied when GPS locations are missing	NSD needs all parts of the curve to have enough data	Missing locations randomly distributed
Journeys and resource extraction can be separated	Not able to identify areas of resource extraction in species without central places	The peak of the curve is the area of resource extraction and only one extraction period occurs before return to the central place
Movement between locations is included	>200 locations/ individual required for an accurate assessment of UD*	Area used during the study represents true use intensity for an individual
Considers use intensity, rather than just use	Cannot identify characteristics of areas which are never used	Features of unused areas do not explain habitat selection
All analyses can be completed in single, free to download, statistical program	Analyses can be computationally time consuming	Researcher knowledge of statistical program R

* Benhamou and Cornélis (2010)

separated by streams which flow into rivers running east to join the Napo and Amazon rivers. The canopy is 10-25m with 30-40m emergents, evergreen and without large disturbances on terre firme, excepting swamps and the flood plains of larger rivers. Rainfall and temperature are aseasonal; average monthly rainfall is <100mm and monthly temperatures vary between 22º and 34ºC (Valencia et al, 2004). When going on a forest trip, members of the community were asked to carry a Mio 168 PDA loaded with Cybertracker (http://cybertracker.org/), and programmed to record a location every 10 seconds. The aim of this study was to determine whether there were behavioural differences between hunters and non-hunters which could potentially be recognised and utilized by prey species to avoid hunting pressure. One point per minute was extracted for analysis to speed processing time. All trips started and ended at the community. Individuals in the community went on forest trips to hunt, fish, gather plants and collect cultivated plants from small forest clearings. For all trips, individuals returned with a single resource (e.g. three monkeys of the same species, or a basket of fish), further supporting the assumption that only a single bout of resource extraction occurred during a trip. The assumption that only the outward journey was spent actively hunting was supported both by the duration of trips (most trips started before 7.30am and lasted approximately 6 hours) and the 96% success rate.

4.3.2. Predictor variables

A small questionnaire was completed before and after each trip, and used to divide trips into “hunting” and “non hunting”. Hunting trips were any trip in which any member of the group carried a gun or blowpipe, regardless of hunting success. The single trip in which an individual took hunting dogs into the forest was also classified as a hunting trip. All non hunting trips returned without meat and included a variety of activities; fishing, collecting wild plants and cultivated plants from small areas of cleared forest, in 14 of 17 non hunting trips individuals took fishing equipment and returned with fish. As mean GPS location error was 30±47m, the study area was divided into 100 x 100m (1 hectare) squares. This scale allows for fine scale analysis and meant recorded locations would be within one square of their actual location. Landscape features were measured as the distance in metres from the centre of each 100 x 100m grid-square to the community and nearest stream and river. Rivers were permanent bodies of water, greater than 10m across, whereas streams were smaller, not navigable by canoe year round, and <5m wide. Shapefiles were imported into R, and distances calculated using the nncross function in the package spatstat 1.23.3.

4.3.3. Modelling methods

39 trips were recorded, but gaps in point collection were common due to the variable forest cover, and any trip where less than 10 points were recorded was excluded (three trips). This left 36 trips for analysis, made up of 19 hunting trips and 17 non hunting trips. These trips had between 15 and 283 GPS locations, representing 32.4±25.5% of expected locations given trip duration. The exact start and end time was identified using questionnaires, and a single point at the centre of community was added at the recorded start and end time for each trip. These additional points meant that net squared displacement (NSD) was calculated from the same point for each trip, and trips were constrained to return to the community even if the end of the trip was not accurately recorded due to battery failure of the PDA unit (six occasions).

Data was modelled using the nlme package of the statistical software R (version 2.13, R core development team 2011). Trip was nested within individual as a random effect to account for individual differences and multiple trips undertaken by the same individual. All variables and combinations were modelled to vary with the random effects. Models were rejected if estimates for any parameter were outside the range of the data, e.g. if θ_r was estimated to occur after the longest trip in the dataset had finished. Models which did not violate these conditions were evaluated using Akaike Information Criteria (AIC, Burnham and Anderson, 2002), whereby lower AIC values suggest a model better explains the data. After selecting a random effects structure, two models were compared: one in which the NSD varied between hunting and non hunting trips, and a second in which NSD did not vary with trip type. The peak of the curve, which represents the furthest distance travelled, was derived from the parameter estimates of the non-linear mixed model.

4.3.4. Habitat selection

The best model for NSD was used to extract locations of resource extraction for hunting and non-hunting trips. When hunting, an individual can be considered searching for prey at any point on the outward journey, only returning when they achieve success. Therefore only the outward journey is part of resource extraction and locations which were part of the return journey were not included (approximated using $t < \theta_r - 2 \times \varphi_r$). In contrast, for non hunting trips, it was assumed that both the out and return journeys were travel to the point of extraction, rather than resource extraction events. Therefore, locations which were part of the outward and return journeys were included (approximated using $\theta_a + 2 \times \varphi_a < t < \theta_r - 2 \times \varphi_r$). Separate UDs for hunting and non-hunting trips were calculated to assess use at the community level, using the biased random bridge method (Benhamou, 2011). For the two individuals with more than 200 locations who conducted hunting trips, and two with more than 200 locations who conducted non-hunting trips, separate UDs using the BRB method were calculated for use with RUFs. If there were no locations for more than two hours, a kernel function was not modelled between the two locations, effectively meaning each trip by an individual was separately modelled. The diffusion coefficient, or smoothing factor, which determines the degree of uncertainty in the location of the kernels between two locations, was calculated from the data using the function BRB.D in the package adehabitatHR version 3.2.2-CAPI-1.6.2. The resulting UDs were analysed using the RUF package version 1.5-1 in R. Following the methods of Kertson and Marzluff (2010), grid squares with use intensity < 99 were selected and the natural log of (100-UD) was used as the response variable to give a normal distribution, whereby larger values meant higher use. The number of grid squares used to estimate the RUF is equal to the 99% probability area of use in hectares, as one hectare = one 100x100m grid cell. The square root of the explanatory variables distance to community (CM), distance to the nearest river (RV) and stream (ST), were used for analysis. These three variables were chosen to give a simple example of using these methods to study habitat selection in humans. Rivers are often used for transport throughout the Amazon region, whereas streams are used for fishing, thus increased use may be expected for non-hunting trips only. Distance from the community was included as most models of human behaviour assume either a uniform circular pattern around the community, or increased use close to the community. Other variables were not included for varying reasons. Not all hunting paths within the study area were mapped, and so hunting paths were not included in the analysis as a variable, and no part of the forest had suffered significant degradation, excepting areas close to the road. Distance to the road was significantly correlated with distance to the community, and community was considered a more informative variable for inclusion in the models. Altitude and slope were digitalised from a paper map, but the variations in altitude within the area used by the community were small (220 – 300 metres) and the paper map did not include sufficiently fine detail to accurately estimate topographical features such as slope, aspect and altitude. Unstandardized coefficient estimates from RUFs can be used to map predicted occurrence of the study organisms within the larger landscape, but standardized coefficients are presented here to show direction of selection and the relative importance of the three explanatory variables. Further details and code for all methods are given in Appendix 3.

4.4. RESULTS

4.4.1. Hunter and gatherer movement: Net squared displacement

Variation in the random effects was mostly due to variation in φ_r, the time at which individuals had completed half the return journey (39.02% of variation explained by differences in φ_r between individuals, and 42.06% by variation within individuals). Differences in the asymptotic height between individuals accounted for less than 0.01% of overall variation, and differences within individuals in asymptotic height accounted for 15.89% of overall variation. For the fixed effects, a lower AIC was found when two separate curves were fitted to hunting and non-hunting trips (ΔAIC: same curve, 507; separate curves, 0). Hunting trips had a higher peak, indicating individuals travelled further when hunting, and also showed a greater time difference between the away and return midpoints, most likely because they were travelling further from the community (Table 4.2, Figure 4.5). Duration of both away and return journeys was shorter for non-hunting trips, but this is to be expected as they travelled less far from the village. In fact, non-hunting trips had a faster travel speed (3.3km/hr for away and return sections) than hunting trips (2.52km/hr when travelling away from the community, and 2.22km/hr on the return portion).

95% confidence intervals of the parameters for hunting and non-hunting trips only overlapped for the mid-point of the return journey (θ_r), and these no longer overlapped at 79% confidence intervals. Locations for habitat selection analyses were extracted using parameter estimates from the model (Table 4.2). Locations before the 273rd minute of a trip ($t < \theta_r - 2 \times \varphi_r$ = 356.42 – [2 x 41.53]) were included for hunting trips, resulting in 1294 locations, and locations were included between the 60th and 265th minute of non-hunting trips ($\theta_a - 2 \times \varphi_a < t < \theta_r - 2 \times \varphi_r$ = 30.58 – [2 x 14.22] <t < 293.44 – [2 x 14.32]), resulting in 1303 locations.

Table 4.2. Estimated trip parameters, with 95% confidence intervals, for hunting and non-hunting trips, determined by modelling net-squared displacement with non-linear mixed effects models.

	Trip Type	
Parameter	**Hunting**	**Non-hunting**
Asymptotic height (δ)	38.00 (26.58 – 49.42)	9.88 (-2.0 – 21.77)
Predicted peak NSD	36.11	9.88
Peak distance travelled (km)	6.01	3.14
Difference between $\sqrt{\boldsymbol{\delta}}$ and peak distance travelled (km)	0.15	0.00
Time of journey mid-point (mins)		
Away $(\boldsymbol{\theta_a})$	69.58 (66.95 – 72.21)	30.58 (25.65 – 35.51)
Return $(\boldsymbol{\theta_r})$	356.42 (311.46 – 401.38)	293.44 (241.15 – 345.74)
Duration of travel between approx $\frac{1}{2}$ and $\frac{3}{4}$ of asymptotic height (mins)		
Away $(\boldsymbol{\varphi_a})$	36.66 (34.98 – 38.35)	14.22 (10.40 – 18.03)
Return $(\boldsymbol{\varphi_r})$	41.53 (38.56 – 44.49)	14.32 (11.67 – 16.97)

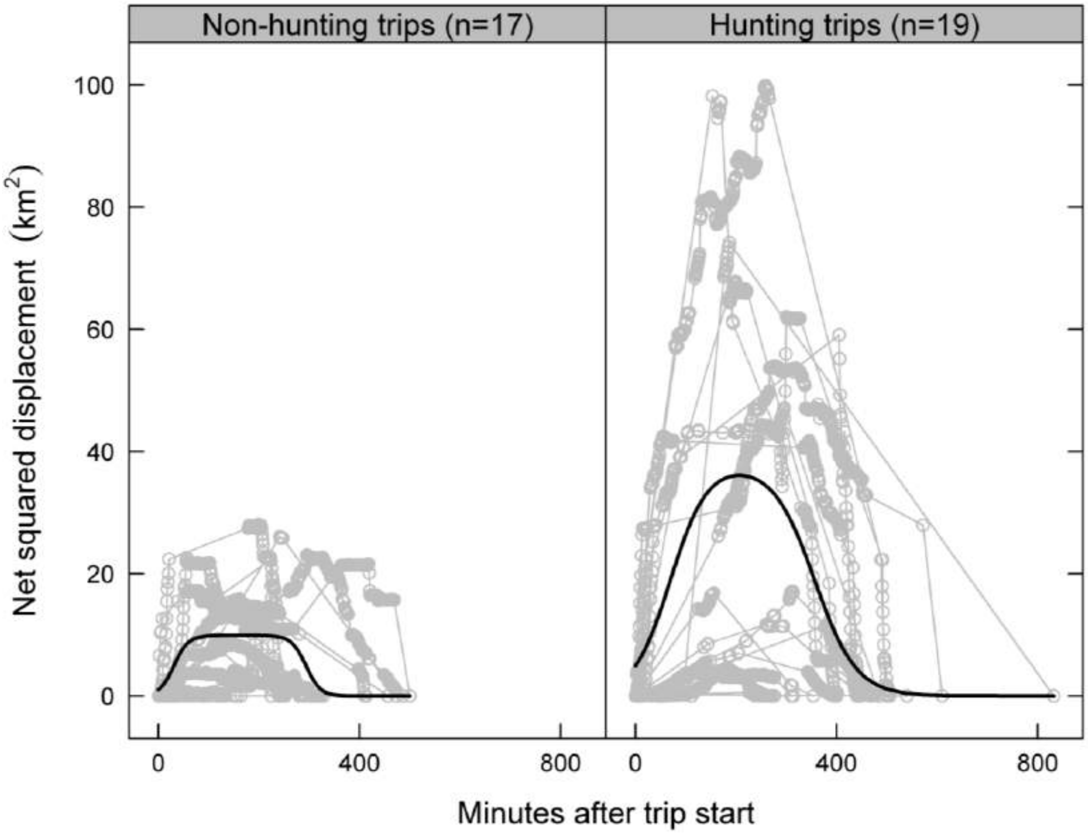

Figure 4.5. Net squared displacement of hunting and non-hunting trips. The grey points connected by lines represent single trips, and the black line superimposed above shows the fitted model.

4.4.2. Use of space by hunters and gatherers: Biased random bridge utilization distribution

For one individual (referred to as individual BA in Table 4.3) where sufficient locations were available for both hunting and non-hunting trips, a greater area was used for non-hunting trips. However, the UD estimate for non-hunting trips by this individual was based on a greater number of trips and locations than the estimate for hunting trips (Table 4.3), and so is unlikely to represent true differences in area used by hunting and non hunting trips.

The pooled overall area for all individuals in the community which was used by hunting trips was greater than non-hunting trips (50% probability of use: 182ha for hunting trips; 99ha for non-

Table 4.3. Number of locations, trips and area of use, with estimates for standardized RUF coefficients for each individual and trip type with sufficient data. Hectares used at 99% probability is equal to the number of grid cells used to evaluate habitat selection. Estimates represent the relationship between the natural log of 100-UD and the square root of the distance to each explanatory variable. Positive values suggest increased use in areas close to the environmental variable, and negative values suggest decreased use in areas closer to the feature. Relative importance of resources is indicated by the magnitude of the estimate for each variable.

Trip Type	**IND**	No. of Trips	**No. GPS locations recorded**	Area of 50% use (ha)	Area of 99% use (ha)	Smoothness	**Spatial range (m)**	Community estimate (±se)	**River estimate (±se)**	Stream estimate (±se)
Hunting	**MA**	11	**838**	194	**1700**	2.3	**367±8**	-0.08±0.03	**-0.14±0.03**	-0.06±0.02
	BA	2	**258**	20	**111**	2.6	**298±22**	0.51±0.20	**-0.85±0.23**	0.35±0.17
Non-hunting	**SS**	4	**433**	45	**396**	1.9	**266±15**	0.04±0.08	**-0.11±0.08**	-0.29±0.07
	BA	4	**386**	44	**549**	2.0	**354±14**	-0.10±0.05	**-0.52±0.05**	-0.26±0.06

hunting trips. 95% probability of use: 1395ha for hunting trips, 689ha for non-hunting trips, Figures 6a and 6b), but this was in part due to a large contribution (both in terms of number of trips and number of locations) from one single individual (Individual MA: 838 of 1303 locations) to the hunting dataset. At 50% probability of use, only 20ha were used by both hunting and non-hunting trips, rising to 263ha at 95% probability of use. This overlap represents between 10 and 40% of the total area used, suggesting that the majority of resource extraction is carried out in areas used exclusively for one type of trip (hunting or non-hunting).

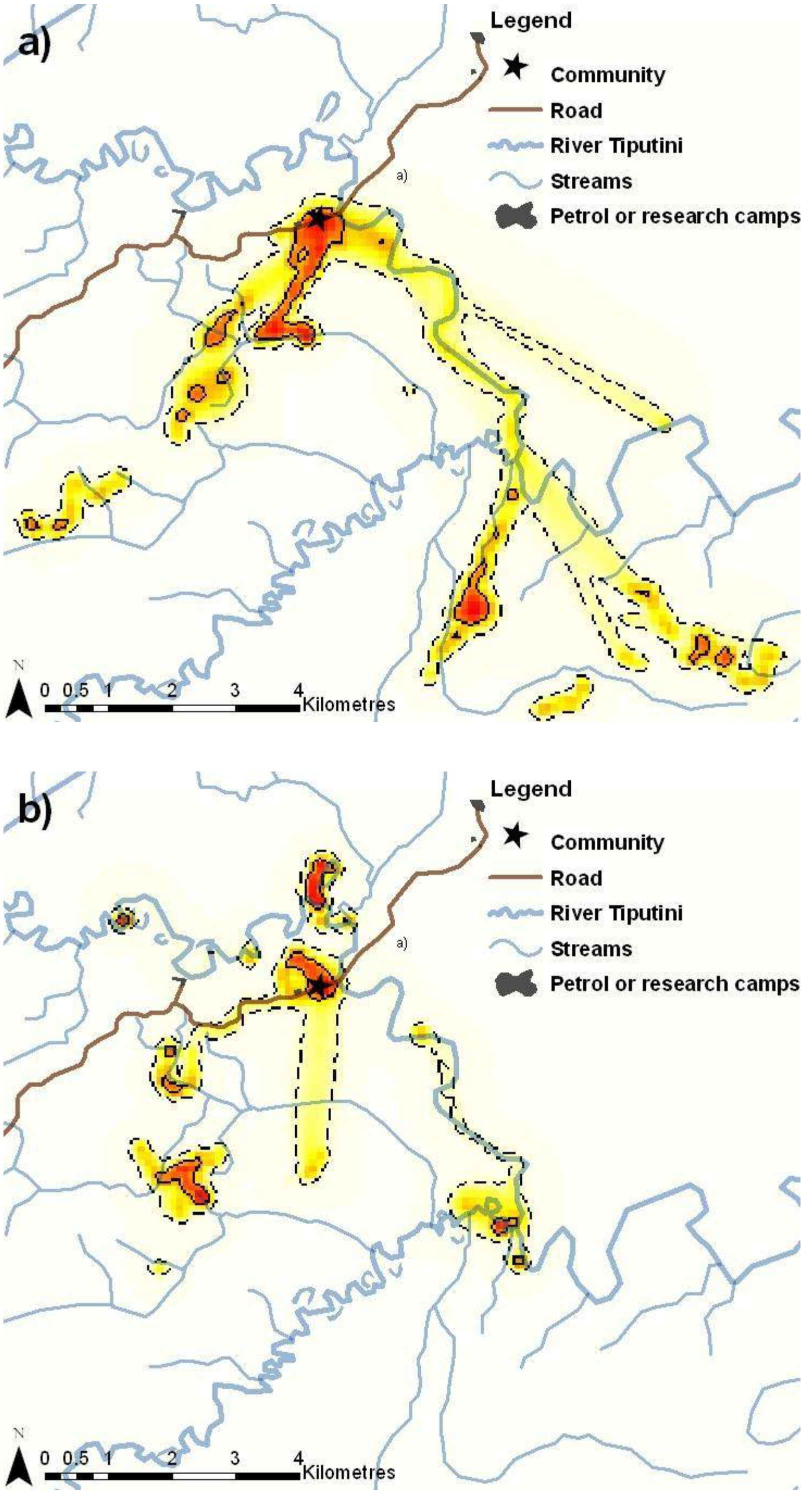

Figure 4.6. Pooled geographical distribution of resource use by all individuals for a) hunting trips b) non hunting trips. Areas more frequently used are darker, with 95% use (dashed line) and 50% use (solid line) contours shown.

4.4.3. Habitat selection by hunters and gatherers: Resource Utilization Function

The number of grid squares used to estimate the RUF for each individual varied between 111 and 1700 (Table 4.3). The most consistent result, for both direction of relationship and relative importance of the explanatory variables was lower use intensity close to rivers (Table 3). Relationship with distance to streams and the community was less consistent. The autocorrelation values of smoothness and spatial range were relatively consistent between individuals, as should be expected as all were using a similar area.

4.5. DISCUSSION

4.5.1 Differences between hunters and non-hunters

We use non-linear models to describe NSD and distinguish movement patterns of hunting and non-hunting trips, with the results showing that treating these two types of trips as distinct is justified by the differences in distance, speed and duration of stay at the furthest point. Asymptotic height varied more within individuals than between individuals, but duration of trip varied both within and between individuals. Insufficient data were available to draw firm conclusions about the nature of area use, overlap and habitat selection in hunters and non-hunters, but these preliminary results suggest that humans do not use a uniform circular area around the community for resource extraction. Furthermore, the few individuals tested suggest that use may not be most intense closest to the community. Both hunters and non-hunters showed less intensive use of areas close to rivers. This is surprising, given the ease of travel along rivers by canoe, and the resources for extraction close to rivers, such as fish and animals such as tapir (*Tapirus terrestris*) and capybara (*Hydrochoerus hydrochaeris*), which use river banks and are eaten in the study area. These preliminary data suggest more research is required into use of space and habitat selection in human resource users.

4.5.2. Net squared displacement

In this example, we used NSD to select locations we considered associated with resource use, but this method could also be used to select other trip characteristics such as removing locations within a certain distance of a central place, or comparing habitat characteristics of the central place and maximum displacement. The modelling process for NSD is flexible, and equations other than the double logistic function (eqn 1) can be used to describe movement. For example, Bunnefeld et al (2011), use the double logistic function, a single logistic function and a linear model to describe NSD and distinguish between migrating, dispersing, and nomadic moose (Alces *alces*) and individuals remaining in a single home range throughout the year. Alternate curves could similarly be used to describe the movement of central place foragers. The advantages of NSD over step-length and turning-angle methods are its ability to account for missing locations, and its definition of cut-points from the data itself. This said, NSD cannot pick up on finer scale variations or pauses in movement, and constant NSD does not mean that an individual is stationary, rather it could be moving equidistant around the point of origin. In future studies, the assumption that active hunting only occurs on the outward trip could be verified by asking hunters to mark the location where they catch their prey.

4.5.3. Utilization distribution built with biased random bridges

To accurately estimate a UD using the BRB method, Benhamou and Cornélis (2010) recommend a minimum sample size of a few hundred serially correlated locations. For the presented data set, this condition is only fulfilled by a few individuals. This high sample of locations needed to estimate UD using BRB is a drawback, but not necessarily a major issue as GPS tracks can generate thousands of locations over the course of a study. The BRB is an improvement over existing kernel methods, as it can incorporate geographical boundaries, estimates a smoothing parameter from the data, and uses algorithms for calculating bridges based on realistic animal movement patterns. Using UD methods which incorporate movement to study human resource users can highlight areas with scant use, which may potentially be acting as source areas in a sink-source system. Calculating overlap between individuals can also help identify if the landscape is being used as a common resource, or if particular areas are only used by certain individuals or types of individuals.

4.5.4. Resource utilization functions

RUFs can identify features associated with both increased and decreased use intensity, which can either be used to describe habitat selection or create predictive maps of use intensity. As RUFs only use presence data, they reduce some of the uncertainty associated with estimation of habitat selection, as neither available nor absent locations are used for comparison.

Furthermore, RUFs associate landscape features with not just observed locations of an individual or species, but also incorporate use intensity, identifying features associated with both increased and decreased use. As these landscape features can be either continuous measures or categorical labels, RUFs offer a very flexible way to determine habitat selection.

4.5.5. Conclusions

Although these methods have been applied to previous studies (NSD: Bunnefeld et al, 2011; BRB: Benhamou, 2011; RUF: Marzluff et al, 2004; Kertson and Marzluff, 2010; Long et al, 2009), they have not previously been used together. This methodological framework tackles some of the major issues for incorporating movement data into studies of resource use. These three methods are the best currently available to study movement ecology and habitat selection where GPS tracking data are available to study human behaviour, but a further advantage of this framework is its flexibility to incorporate methodological advances. For example, if a new method is developed for estimating utilization distributions, this can be substituted for the BRB within the framework. Alternatively, if a study has fewer than the 200 relocations per individual recommended for BRB, a simpler UD estimation method can likewise be substituted. The use of these methods has demonstrated how differences between hunters and non hunters in a single community can be quantified, and provided preliminary results which suggest further research is required into some of the assumptions about human resource users.

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Chapter 5

Hunted woolly monkeys (*Lagothrix poeppigii*) show threat-sensitive responses to human presence

5.1 INTRODUCTION

5.1.1 Anti-predator responses

Anti-predator responses can be costly, reducing time available for feeding and other activities, or incurring physical costs from energy expenditure or injury (Lind and Cresswell, 2005). These costs can be reduced if prey are able to distinguish between dangerous and non-dangerous individuals of a single predator species. Not all encounters of prey with predators will be predation events. This may occur for a number of reasons; for example because the predator has recently fed, or if the prey gives alarm calls to a stalking predator and disrupts the hunt (Gil-da-Costa 2007). If prey respond with anti-predator strategies to all encounters with a particular species, they may incur significant costs, particularly if the predator is common but attacks are infrequent. Prey which can distinguish between dangerous and non-dangerous individuals of a predator species and respond appropriately will reduce the costs of anti-predator behaviour (Bishop and Brown 1992). This threat sensitive predator response, coined by Helfman (1989), involves the prey altering their response depending on the magnitude of the threat. In general, this translates to increased responses when the threat, and therefore risk, is greatest. This effect has been demonstrated in damselfish (Helfman 1989), elephants (Bates et al. 2007) and larval treefrogs (Puttlitz et al. 1999).

5.1.2 Humans as predators

Humans are an example of a common predator which does not always attack, and so are a predator to which threat sensitive responses would be particularly appropriate. Humans are also the main predator of some primate species, yet have received relatively little attention compared with carnivorous mammals and raptors (Urbani 2005). Zuberbuhler et al. (1997) used human model experiments and showed that Diana monkeys (*Cercopithecus diana*) responded to humans cryptically. However, a later study showed Diana monkeys giving calls in response to human models (Zuberbühler 2000). Arnold et al. (2008) also suggest inconsistent reactions to human presence in putty-nose monkeys (*Cercopithecus nititans*) in Nigeria. Response to the presence of a moving human was cryptic behaviour in 16 of 22 experiments, but groups called during the other six experiments. Cryptic trials were excluded from analysis in the paper, with the authors arguing that it was not possible to conclude the monkeys had seen the stimulus if they did not call. However, the same silent response was observed in far fewer cases to other stimuli (moving leopard 0/11, stationary eagle 2/10, stationary leopard 4/21), arguably suggesting the monkeys had detected the human stimulus, but were responding to it cryptically. A study by Croes et al. (2006) in Gabon did not find differences between hunted and unhunted areas in the number of monkey groups which called in response to human presence, but did find that monkeys in areas with hunting pressure were more likely to flee. As human hunters are generally pursuit rather than ambush hunters and may try and hunt any (but not all) desirable prey they encounter (Zuberbuhler 1997), it is perhaps surprising that primates should show anything but a cryptic response to humans.

Zuberbühler & Jenny (2002) argue that in comparison with other predators, high levels of human offtake are evolutionarily recent, so primates have no evolved response and hence respond inconsistently. An alternate hypothesis to explain these seemingly inconsistent primate responses to humans is that primates are showing a threat-sensitive predator response. Monkeys in these studies could have been responding to additional behavioural cues from the humans which suggested different levels of threat. Cryptic behaviour is likely to be the best anti-predator strategy against human hunters (Zuberbühler 2007), but appropriate responses to other humans may depend on the characteristics of the humans present. For example, if humans are fishing or conducting other activities below the monkeys for some hours, it may be more appropriate to flee immediately and not waste time freezing. Distinguishing between different humans in this way would reduce the costs of primate anti-predator responses to this common predator, but assumes that prey are able to distinguish between individuals of a single species, and react appropriately. Although wild prairie dogs (Slobodchikoff et al, 1991) and elephants (Bates et al. 2007) have been shown to distinguish between types of human, no previous research has been conducted to determine if primates can make this distinction.

It has been argued that prey which live in groups benefit from the lower individual vigilance effort which is required (Roberts, 1996), and there is a lower probability of each individual being attacked during a predation attempt (Treherne and Foster, 1982). However, human hunters may try to catch multiple individuals during a single predation attempt. If one individual attracts attention, for example by calling, all individuals are at risk. Therefore, for the individual, following the response of other individuals in the group is likely to be the best strategy. If all individuals are freezing, except one which flees, that individual will be the most obvious and experience increased predation risk. Likewise, if all other individuals are fleeing and one individual freezes and is visible, it will be an easier target for a hunter.

5.1.3 Predictions of the threat sensitive predator response hypothesis

Here I examine whether primates can use predator behavioural cues to distinguish dangerous and non-dangerous individuals of the same species. I focus on primates because they are often preferred human prey species due to their relatively large size and conspicuousness, and are often vulnerable to overhunting due to their social nature and low rates of population increase (Mittermeier 1987). Primates are also particularly interesting as they are good candidates for showing a threat-sensitive response to humans, but this has not yet been tested. The specific study site in the Ecuadorian Amazon was chosen as one that had areas with both high and low hunting pressure, but in which hunting pressure was not so great that primates were extirpated in the hunted area. In particular, I assess responses to dangerous and non-dangerous humans. Based on the hypotheses that hunted monkeys respond to human presence consistent with the threat-sensitive predator response hypothesis, three predictions were tested:

1) Behaviour changes after exposure to human presence, in a manner consistent with a threat response (e.g. in a way that reduces detectability or by fleeing);
2) The strength of this response is a function of the perceived magnitude of the immediate threat, based on the simulated behavioural characteristics of the human present (hunter, gatherer or researcher);
3) The strength of this response is a function of the perceived magnitude of the underlying threat; based on differences in prior exposure to different threat types (high and low pressure hunting areas).

5.2 METHODS

5.2.1. Site and Species

Experiments on unhabituated monkeys were conducted in Yasuní National Park, Amazonian Ecuador. Two sites 26km apart were used, one with higher hunting pressure (HP, Yasuní Research Station) and another with lower hunting pressure (LP, Tiputini Biodiversity Station). In the study system, monkeys are likely to encounter three types of human: hunters, gatherers and researchers. Of these, hunters pose the greatest threat as they are actively searching for prey, and carry lethal weapons. Gatherers do not pose a lethal threat, but may be collecting resources as part of a mixed group of hunters and gatherers, or return to the community and report the location of the group to hunters (Appendix 1). Researchers pose no lethal threat to monkeys, but may follow groups or even on occasion dart monkeys. For this study we make the assumption that woolly monkey encounters with hunters are likely to be lethal, encounters with gatherers may be associated with (time-delayed) lethalness, and encounters with researchers are never likely to be lethal. Each experiment simulated the presence of one of these three types of human behaviour.

Poeppigi's woolly monkeys (*Lagothrix poeppigii*) were used for the experiments are they are a preferred prey species in the study area (see chapter 3) and in the Amazon in general (Peres 1991). They experience higher hunting pressure at the HP site, with an estimated hunting offtake of over 200 individuals per year from an area around 759.2km^2 (derived from Franzen, 2006). Hunting has not been observed at the LP site by staff of Tiputini Biodiversity Station, although hunters did report hunting in the surrounding areas (S. Papworth, unpublished data). As woolly monkeys are highly mobile, it is impossible to state that individuals at Tiputini Biodiversity Station have not experienced hunting pressure, thus the site is classified as having "low hunting pressure" rather than being "unhunted". Both sites are used by researchers, though Tiputini Biodiversity Station generally has more researchers present than Yasuní Research Station.

The average weight of hunted woolly monkeys is 6.1kg (from Franzen 2006), and even though harpy eagles and jaguars prey on similar-sized howler monkeys and are likely to prey on woolly monkeys, there is only one published record of non-human predation on woolly monkeys (Ferrari 2009). Woolly monkeys live in large, social groups that can be widely dispersed in the forest. In the study area at the HP site, sub-groups (groups separated by at least 50 – 100m and encountered 10 minutes apart, as defined by Derby, 2008) average 9.5 individuals, with a population density of 20.4 individuals per km^2. Sub-groups at the LP site average 7.9 individuals and have a population density of 31.8 individuals per km^2 (Derby 2008), although true densities at this site may be far higher (A. Di Fiore, personal communication).

5.2.2 Experimental conditions

A human behaving according to each of three conditions was presented to seven groups over the course of a year, three groups at the HP site and four at the LP site, giving a total of 21 experiments. It was not possible to conduct these experiments on a greater number of groups due to difficulties locating additional groups in other areas at the HP site and the habituation of groups in all other areas at the LP site. Although all individuals in this study are likely partially habituated to the presence of researchers due to their location around two research stations, care was taken that experiments were conducted outside the area in which woolly monkeys have been intensively habituated by Proyecto Primates (https://webspace.utexas.edu/ad26693/www/yasuni/index.html). At the LP site, experimental protocol stated that if any member of the group was observed to have a radio collar, indicating they were part of this project, experiments were not conducted on the group.

To ensure each condition was presented to seven independent groups, one experiment of each type of human behaviour was conducted in each of seven areas. Experiments in the same area were separated by a minimum of nine days (inter-trial duration median = 69.5 days, range = 9-199 days). Each area was separated from others by a minimum of 1km and separation distances less than 1.5km only occurred when physical barriers such as roads or rivers also existed between locations (Figure 5.1). During experiments it was not possible to identify individuals, as group members were infrequently visible. Woolly monkeys live in large social groups with overlapping territories which spread over large areas during the day (Di Fiore 2003). Although it is possible that some individuals in each area experienced all three conditions, experiments in a single area were never conducted on the same number of individuals, and experiments recorded group, rather than individual level behaviours. As autocorrelation in a single experiment was considered a greater source of potential error than the possibility that some individuals experienced more than one experiment, generalised estimating equations were used for analyses.

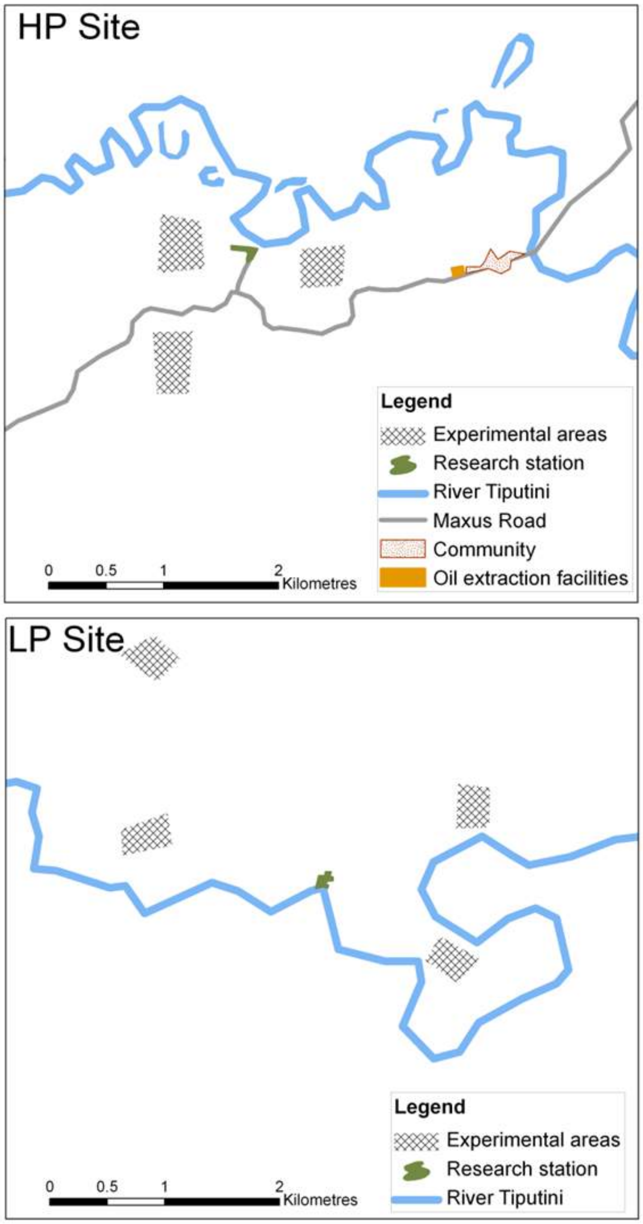

Figure 5.1. One experiment of each type (hunter, gatherer and researcher) was conducted in each of the experimental areas used at the two sites (HP site = high hunting pressure, Yasuní Research Centre; LP site = low hunting pressure, Tiptutini Biodiversity Station).

5.2.3 Experimental procedure

Data from pilot experiments indicated groups took a minimum of 20 minutes after encountering a human to return to baseline behaviour as recorded before human presentation, a 30 minute observation period after the appearance of a human was used, balanced with 30 minutes of baseline data before experimental presentation. On each morning, a target area and condition type was assigned before entering the forest. Groups were located by both sight and sound. On occasion, movement was heard in the trees so SP and a field assistant hid silently nearby in thick vegetation until the species could be confirmed from calls or by sight. If SP or the field assistant were seen by the monkeys before the experiment started, or made any loud noises, both moved to a location within hearing distance of the group and hid out of sight for two hours before starting the experiment (n=1). At the start of the experiment, SP and the field assistant hid in the undergrowth and groups were observed for 30 minutes at a distance of 5-20 metres to determine baseline behaviours before the stimulus was presented. Experiments were abandoned if groups noticed the experimenters in this time. To begin the stimulus, the field assistant walked under the group, behaving as one of the three types of human outlined in Table 5.1. Key differences between

Table 5.1. Human behaviour associated with each experimental condition.

	Hunter	Gatherer	Researcher
Equipment	2.4m blowpipe 50cm dart quiver	None - collecting leaves / seeds from the forest floor and low shrubs while moving	Small notebook / small bag / binoculars / video camera
Noise level	Very quiet / silent	Normal	Normal
Movement	Slow, aiming the blowpipe at them when directly underneath	Moving from plant to plant below the monkeys, stopping to collect.	Moving around below the monkeys, stopping underneath when directly visible.
Gaze direction	Looking up at monkeys	Looking down and ignoring monkeys	Looking up at monkeys

the conditions were silent movement and the presence of a blowpipe for the hunter condition, louder movement and gaze direction away from the monkeys whilst collecting plant material in the gatherer condition, and louder movement and gaze direction towards the monkeys for the researcher condition. During the study, the area and experiment type were balanced between two assistants, and area and experiment type were determined before entering the forest each day. Therefore, individuals in each of the seven areas could have experienced a maximum if two exposures to a single assistant, and it is unlikely that they would recognise the assistant and that this could affect the outcome of the trial. After five minutes, the field assistant moved away silently and out of sight. It is not possible to know exactly when the monkey group first saw or heard the stimuli (the assistant), but it is assumed that one or more individuals noticed the stimuli within these five minutes. Behaviour was then observed for a further 25 minutes after the removal of the stimulus. Group behaviour was recorded using presence/absence of travelling or visibility of any group member in five minute intervals. Height range, number of individuals detected, visibility of individuals, group spread and if any individuals had called or travelled (movements greater than 5m or between trees) were sampled. All vocal behaviour of the group was recorded with a Marantz PMD661 Professional Portable SD Field Recorder and Seinnheiser ME67 directional microphone. Direction of movement was recorded with a compass and experiment duration with a Casio wristwatch.

5.2.4. Calculations

Visibility was calculated using the methods of Koné (2004), although initial analyses showed that monkeys were only visible in 65 of 252 five minute segments, so a binomial distribution was used as a response, with the group either coded as “visible” or “not visible”. The group was coded as visible if any part of any monkey was visible at any point during a 5 minute segment. In order to calculate the number of calls produced, sound recordings of the experiment were first digitalised, and then cut into five minute segments. In order to allow the five-minute segments to be coded impartially with the coder blind to the condition and period, each five minute segment was initially dummy labelled by the field assistant before the data were coded by SP. Number of calls was determined for each five minute section audibly and confirmed with inspection of the waveform and spectrogram of the sound in the program PRAAT (Boersma, 2001). A more fine-grained analysis of the immediate vocal responses was also conducted, and the number of calls for each minute was calculated for the 5 minute sections immediately before, during and immediately after experimental presentation. As calls are graded and no rigorous description has been produced for wild populations of woolly monkeys, calls were not separated into call types.

5.2.5. Baseline differences between sites

During each experiment, it took a median of 30 minutes (range 0-60) to detect all members of the group in the immediate area and estimate the size of group likely to detect the stimuli. It is possible that some individuals were not detected during the experiment. Only independently-locomoting animals were included in this estimate. Spread and median height of detected animals were estimated during the experiment by SP and the field assistant. When additional group members were detected at the periphery of the previously detected sub-group during the experiment, estimated spread among the detected animals increased. Median estimated height also changed when additional group members were detected. For this reason, height and spread were not included as behavioural measures which could change before and after experimental presentation. The latency in detection of all group members does not, however, change the validity of observations of calling, travelling and visibility. Even if group members are not immediately detected, they would be detected if they called, travelled or moved to a location where they were visible.

5.2.6. Analysis

All analyses were conducted using the statistical program R (version 2.14.1, R core development team 2012). Group size and median estimated group height and spread before experimental presentation were compared between the two sites using a Wilcoxon rank sum test, which is identical to the Mann-Whitney U test (non-parametric test for comparison of independent data).

Previous studies on primate responses to humans have used non-parametric analysis methods, and only recorded observed behaviour after the presentation of humans. This is partly as these studies aimed to compare loud-calling responses between predator types (Zuberbuhler et al. 1997; Arnold et al., 2008) or were observational (Croes et al., 2006). This study aims to compare primate antipredator responses to different types of human behaviour, thus the crucial contrast is the change in behaviour from before experimental presentation to afterwards.

To compare responses to the presence of humans, generalised estimating equations with the package geepack were used (Halekoh, Højsgaard, and Yan 2006). Generalised estimating equations are semi-parametric regression techniques which perform consistently even under mild violations of the specified variance structure (Hardin and Hilbe, 2003), such as data which do not perfectly conform to a Poisson distribution. Subsequent observations in each experiment (five minute sample periods) were likely to be related as members of the group responded to the activity of others (e.g. responding to calls), so generalised estimating equations with an auto-regressive AR1 correlation structure were used. Failing to account for this autocorrelation would increase the chances of a false positive result. For each behaviour measured, the correlation between sequential periods is shown. Correlation is shown as a probability (including the standard error) that an observed behaviour is the same as the previous period. Three explanatory variables and their interactions were used for all models and a summary of the implications of including each of these variables and interactions in the final model is given in Table 5.2.

From all possible models nested in the global model, nine models were selected which tested the specific hypotheses of the study. In particular, condition was only included in models in interaction with experimental period, as I was interested in changes in behaviour as a result of experimental manipulation and how that varied across stimulus types. Models were compared using QICu, a quasi-likelihood version of AIC which is appropriate to the quasi-likelihood methods of generalised estimating equations. QICu and ΔQICu for all nine models are presented in Appendix 3. Post-hoc Wald tests were conducted on the best model using the R package contrast (Kuhn, 2011) to determine which experiment types showed significant behavioural differences between the period before and after experimental presentation. For immediate calling response, three periods were used: before, during and after experimental presentation. As generalised estimating equations were used, the period during experimental presentation was included to allow continuity for the AR1 correlation structure. Post-hoc Wald tests compared the immediate calling response in the five minutes before and after experimental presentation as it was not possible to know at which point during the experimental presentation the field assistant was first observed. Difference in behaviour after experimental presentation is graphed on a logit scale of probability for binomial variables and a log scale for Poisson variables in order to display standard errors.

*Table 5.2. Explanatory variables and interactions included in the maximal model and the interpretation of these if included in the final model. Condition (hunter, gatherer or researcher); Period (before and after experimental presentation); Site (HP or LP). * Periods are before, during and after for immediate calling response – see text for more details.*

Variable	**Interpretation of inclusion in final model**
Condition	Behaviour differs depending on the type of human presented
Period*	Behaviour differs before and after experimental presentation (EP)
Site	Behaviour differs between sites
Condition x Period	Behaviour before and after EP differs depending on condition
Site x Period	Behaviour before and after EP differs depending on site
Condition x Site x Period	Behaviour before and after EP differs with condition, and these differences also differ between sites.

5.3 RESULTS

5.3.1. Baseline differences in height, group size and spread

Median number of animals detected was 10 (interquartile range 7-15), and did not differ between sites (Wilcoxon rank sum, $N_{HP\ site}$=9, $N_{LP\ site}$=12, W = 31, P=0.11). Median height of these detected animals before experimental presentation was 16.50m (interquartile range 14.17-20.00m), and no difference between sites was found (Wilcoxon rank sum, $N_{HP\ site}$=9, $N_{LP\ site}$=12, W = 36, P=0.21). Median estimated group spread was greater at the HP site than the LP site (Wilcoxon rank sum, $N_{HP\ site}$=9, $N_{LP\ site}$=12, W = 89, P=0.013, $median_{LP\ site}$ = 55m, range=45-70, $median_{HP\ site}$=45m, range=35-60).

5.3.2. Immediate calling response

To describe immediate calling response of woolly monkeys to human presentation, the best model included all interactions, and significant autocorrelation (0.648±0.11) between sequential observations in the same experiment. After being presented with humans behaving as hunters, calling decreased at both sites, but no significant response to researchers was observed at either site. After presentation of the gatherer condition calling increased at the LP site but decreased at the HP site (Figure 5.2).

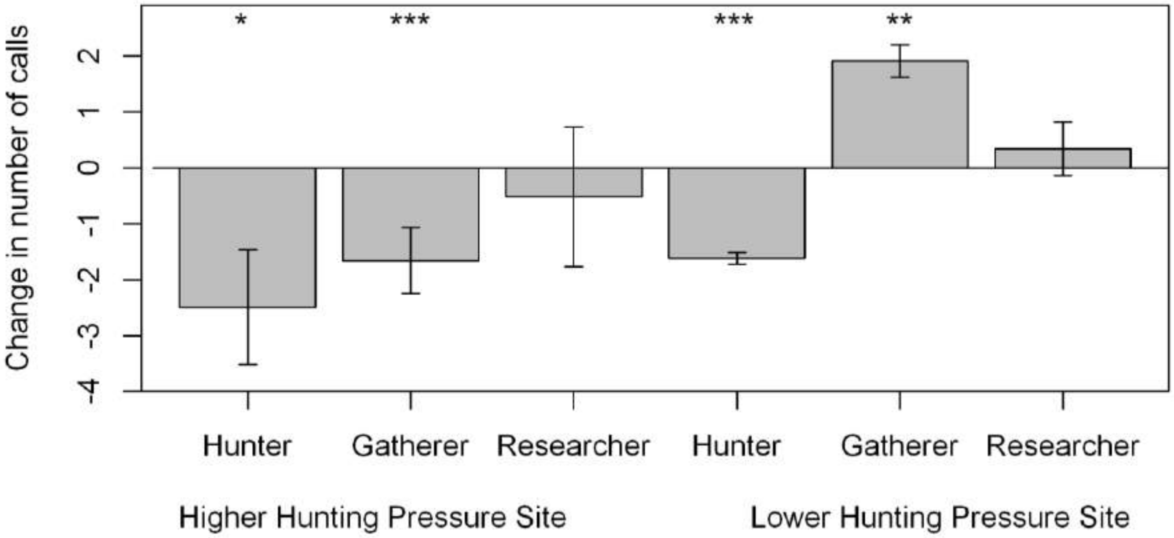

*Figure 5.2. Immediate calling response: Change in number of calls (log scale to allow standard errors to be displayed) given in the five minutes immediately after experimental presentation when compared with the five minutes immediately before. Error bars show standard errors of the estimate. P values of differences between the period before and after experimental presentation are shown: * p=0.05-0.01, **p=0.01-0.001, ***p<0.001. Hunter condition: Wald test, HP site: Z = 2.42, df = 1, p=0.016; LP site: Z = 15.3, df = 1, p < 0.001. Gatherer condition: HP site: Wald test, Z = 2.8, df=1, p=0.005, LP site: Wald test, Z = 6.6, df = 1, p<0.001. Researcher condition: Wald test, p>0.05 for both sites.*

5.3.3. Short term responses

Number of calls

To describe the number of calls in each five minute block throughout the experiment, the best model included all interactions, and a correlation of 0.32±0.13 between sequential observations in the same experiment. After experimental presentation, the number of calls decreased in response to most conditions. Number of calls decreased at both sites after presentation of hunters. After presentation of the researcher condition, number of calls decreased at the LP site but increased at the HP site. In response to the gatherer condition, no response was observed at the LP site, but number of calls decreased at the HP site (Figure 5.3).

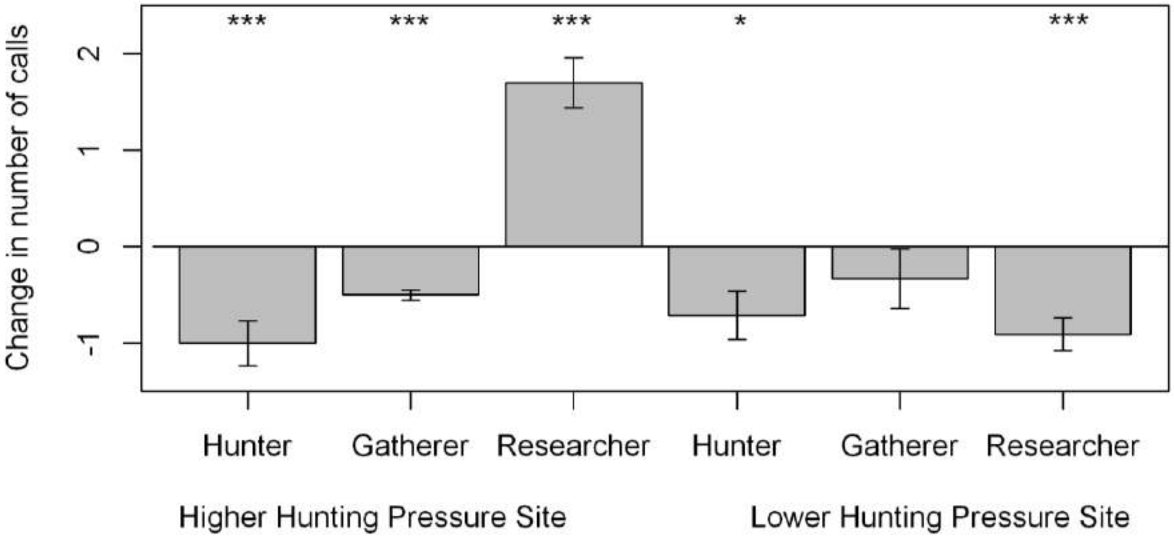

*Figure 5.3. Change in number of calls (log scale to allow standard errors to be displayed) given in the 30 minutes after start of experimental presentation, compared with the previous 30 minutes. Error bars show standard errors of the estimate. P values of differences between the period before and after experimental presentation are shown: * p=0.05-0.01, **p=0.01-0.001, ***p<0.001. Hunter condition: Wald test, HP site: Z = 4.26, df = 1, p<0.001; LP site: Z = 2.84, df = 1, p = 0.045. Researcher condition: Wald test, HP site: Wald test, Z = 6.53, df=1, p<0.001, LP site: Z = 5.23, df = 1, p<0.001. Gatherer condition: Wald test, HP site: Z = 10.3, df=1, p<0.001, LP site, p>0.05.*

Travelling

The best model included all interactions, and a correlation of 0.54±0.09 between sequential observations in the same experiment. Significant decreases in travelling after experimental presentation of humans behaving as hunters was observed at both sites, and a significant decrease in travelling was also observed at the HP site in response to humans behaving as gatherers. All other experiment types showed no significant difference in travelling after experimental presentation (Figure 5.4).

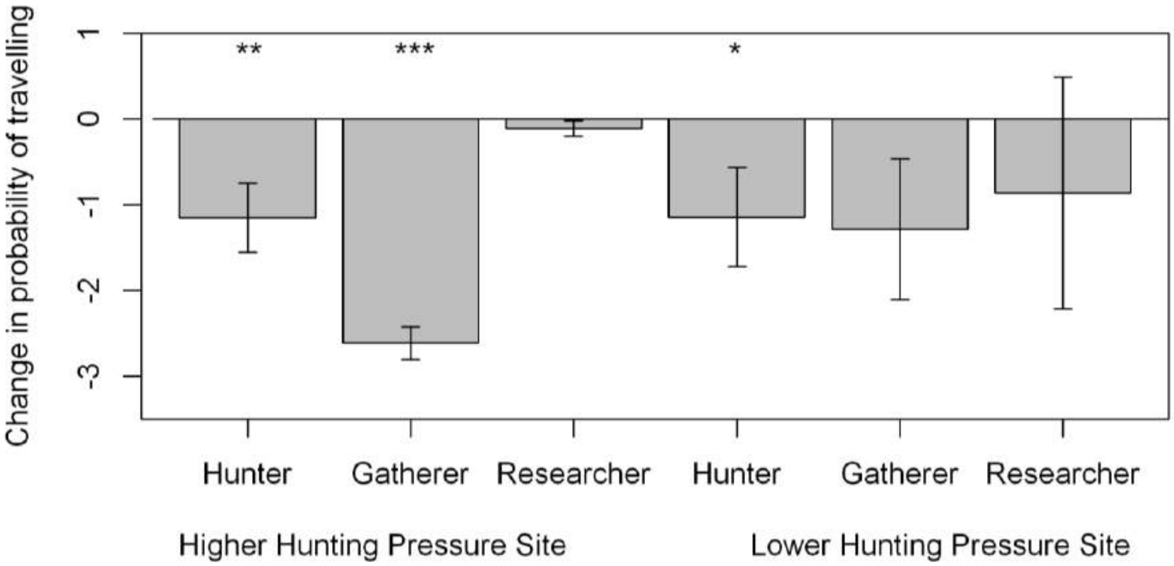

*Figure 5.4. Change in probability of travelling (logit scale to allow standard errors to be displayed) in the 30 minutes after start of experimental presentation, compared with the previous 30 minutes. Error bars show standard errors of the estimate. P values of differences between the period before and after experimental presentation are shown: * p=0.05-0.01, **p=0.01-0.001, ***p<0.001. Hunter condition: Wald test, HP site: Z = 2.86, df=1, p=0.004; LP site: Z=1.96, p = 0.05. Gatherer condition: Wald test, HP site: Z = 13.6, df=1, p<0.001, LP site, p>0.05. Research condition: Wald test, both sites, p>0.05.*

Visibility

The best model to describe visibility during the experiment included all three main effects, an interaction between condition and time period, and high autocorrelation of 0.58±0.06 between sequential observations in the same experiment. No interaction between site and experiment period was found, but throughout all experiments, visibility was lower at the HP site (Wald test, Z = 2.07, df=1, p=0.038). Visibility did not increase after experimental presentation for any condition, but only showed a significant decrease after experimental presentation of the hunter condition, and in response to the researcher condition (Figure 5.5).

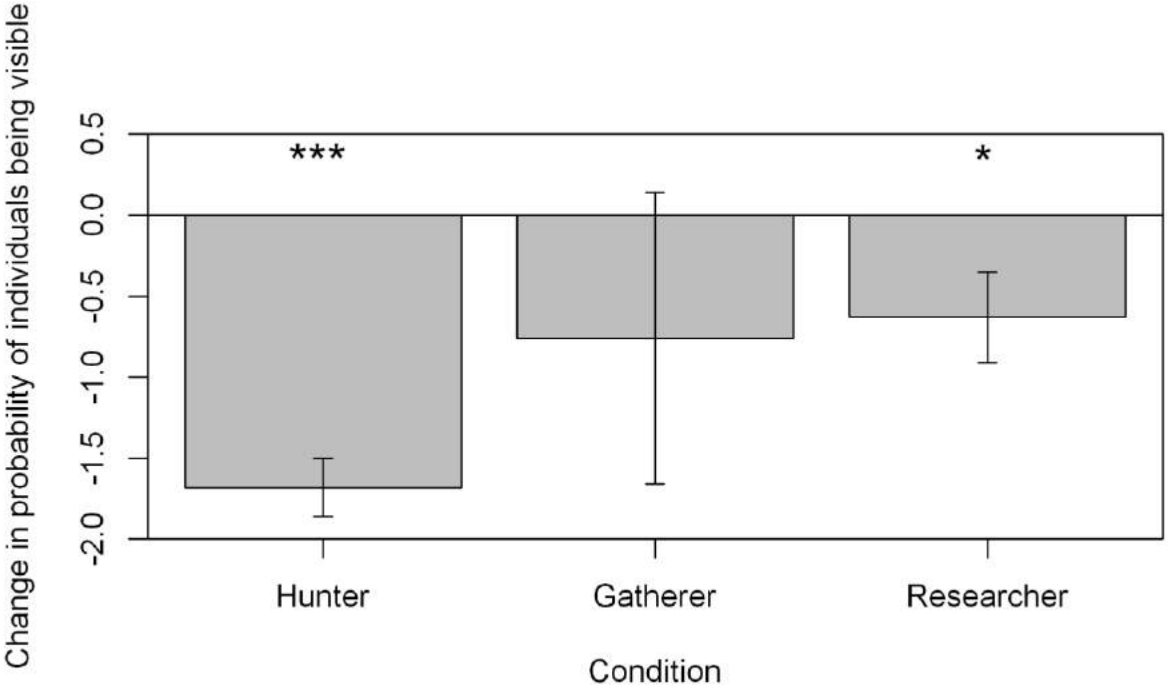

*Figure 5.5. Change in probability any individual in the group being visible (logit scale to allow standard errors to be displayed) in the 30 minutes after start of experimental presentation, compared with the previous 30 minutes. Data from both sites is shown. Error bars show standard errors of the estimate. P values of differences between the period before and after experimental presentation are shown: * p=0.05-0.01, **p=0.01-0.001, ***p<0.001. Hunter condition: Wald test, Z = 9.17, df=1, p<0.001. Researcher condition: Wald test, Z = 2.3, df=1, p=0.022. Gatherer condition: Wald test, p>0.05.*

5.4 DISCUSSION

5.4.1 Responses to experimental presentations

Changes in woolly monkey behaviour were observed after presentation of human models at both sites, and some degree of change was observed in response to all conditions (Table 5.3). However, these changes differed with both site and experimental condition, with all responses differing with condition presented. At both sites the strongest response was shown to the hunter condition, with all measures showing significant decreases in behaviour in response to experimental presentation. At the HP site, the next strongest response was to humans behaving as gatherers, with three of

Table 5.3. Direction and strength of changes in behaviour after experimental presentation, and whether the observed behavioural change supports the threat sensitive predator response hypothesis. Calling responses are displayed on a log scale, and probability of travelling and being visible are on a logit scale so standard errors can be displayed. Significant changes in behaviour are shown in bold.

	High pressure site			Low pressure site		
Behaviour	Hunter	Gatherer	Researcher	Hunter	Gatherer	Researcher
Threat level	High	Intermediate	Low	High	Intermediate	Low
Immediate calls	**-2.49±1.03**	**-1.66±0.59**	-0.52±1.25	**-1.62±0.11**	**1.91±0.29**	0.34±0.48
Calls	**-1.00±0.23**	**-0.50±0.05**	**1.70±0.26**	**-0.71±0.25**	-0.33±0.31	**-0.90±0.17**
Travel	**-1.15±0.40**	**-2.61±0.19**	-0.11±0.09	**-1.14±0.58**	-1.28±0.82	-0.86±1.35
Visibility	**-1.68±0.18**	-0.76±0.90	**-0.63±0.28**	**-1.68±0.18**	-0.76±0.90	**-0.63±0.28**
Supports hypothesis	Yes			No		

four measures showing decreases in observed behaviour, and the least pronounced response was to the researcher condition, where just two measures showed change; an increase in calling and a decrease in visibility. In contrast, the lowest response at the LP site was to the gatherer condition, with just a short term increase in calling, and there was a greater response to the researcher condition, with a decrease in visibility and longer term decrease in calling.

Responses to the hunter condition showed a consistent decrease in all measures of behaviour at both sites. This suggests that woolly monkeys were responding to hunters cryptically, which is an appropriate response for pursuit hunters, which cannot be deterred by mobbing or other active anti-predation strategies (Zuberbühler et al. 1997). There was also a generally cryptic response to the gatherer condition at the HP site, but unlike the response to the hunter condition, there was no significant decrease in visibility. Interestingly, although a decrease in visibility in response to the researcher condition suggested a cryptic response, an increase in calling was observed in the 30 minutes after experimental presentation. This increase in calling may be an increase in contact calls as individuals confirm the location of other group members (Rendall et al, 2000). A short-term increase in calling was also observed at the LP site, but in response to the gatherer condition. Responses to the researcher condition at the LP site again suggested a cryptic response, with calling and visibility decreasing.

5.4.2 The threat-sensitive predator response hypothesis

Results at the HP site are in agreement with the predicted threat-sensitive predator response, as greater changes in behaviour were observed in response to more threatening humans. Although monkeys at the LP also showed greatest change in response to the hunter condition, they did not show the predicted greater response to humans behaving as gatherers than humans behaving as researchers. This may be because monkeys at the LP site are naive, and have insufficient experience with the three types of human presented to respond as predicted. Nevertheless, reactions to hunters were consistent with reactions at the HP site and reactions to each condition were distinct, so woolly monkeys at the LP do not appear to assess all humans in the same way. Alternately, woolly monkeys at the LP site may lack experience specifically with gatherers, and so do not respond appropriately to their presence. Gatherers use areas closer to the community and make shorter trips (Papworth et al. 2012), so it is plausible that woolly monkeys at the LP site (more than 10km from the nearest settlement, compared with around 2km at the HP site) are less exposed to gatherers. Likewise, the HP site generally has fewer researchers, and most of these work in a single 50ha plot. This lack of knowledge may explain the paradoxical increase in calling response at each site, as group members may vocalise in response to the novel condition.

An alternate explanation for this unexpected result at the LP site may be that relative threat for each human condition is not consistent for the two sites. At the HP site, it is not unreasonable to make the assumptions of this study in terms of the relative lethal threat posed by each condition – hunters are immediately and lethally threatening, gatherers are potentially lethally threatening, and researchers pose no mortal threat. However, at the LP site, darting of various primate species, including numerous woolly monkeys, has occurred to attach radio collars, and several dozen woolly monkeys in the area have had small amounts of tissue extracted with non-lethal biopsy darts (Di Fiore and Fleischer 2005; Di Fiore et al. 2009). As a result of this, researchers could be considered greater threats than gatherers at the LP site, even though these biopsy darts are non-lethal. By contrast, only two woolly monkey females, and no other species, have experienced biopsy darts in the HP study area, and this occurred in 1998 (Di Fiore and Fleischer 2005). Researchers may therefore be perceived as more threatening than gatherers for woolly monkeys at the LP site due to the higher levels of darting which have occurred. Quantitative data on the response of woolly monkeys shot with a poisoned arrow or biopsy darts are unavailable, but if these responses are similar, non-targeted individuals may associate the auditory and visual cues from the shot monkey with the presence of both hunters and researchers. Although this is speculative, if these, or other similarities exist, woolly monkeys at the LP site may be showing a response consistent with perceived threat levels. Biopsy darting no longer occurs at the LP site due to advances in DNA extraction techniques, but as woolly monkeys can live up to 30 years (Morand and Ricklefs 2005), those who have experienced this procedure may still present in the population. Although experiments were not conducted on collared individuals, the darting took place on various groups at the LP site, and individuals who experienced darting may have migrated to groups with which these experiments were conducted.

These results, and the threat sensitive predator response hypotheses, could explain previously noted variability in primate reactions to humans. In this study, woolly monkeys generally responded cryptically, but an increase in calling was observed to the possible least threatening condition at each site. Arnold et al. (2008), Zuberbühler et al. (1997) and Zuberbühler (2000) do not give details about the behaviour of their human models, but variations in behaviour of these human models in their studies could have resulted in the differing responses observed. The unexpected responses of fleeing and calling found in the study of Croes et al. (2006) could be because monkey groups were correctly assessing those conducting the research as researchers. From the results of this study, it is unclear which cues woolly monkeys use to distinguish different classes of humans. The behaviours associated with each condition were designed to simulate the differences between hunters, gatherers and researchers, rather than determine which cues are used by monkey groups. K. Zuberbühler (personal communication) suggested that groups respond differently based on the gaze direction of humans, but this hypothesis is not supported by the observed results in this study. It is likely that the large, 2.4m blowpipe is a reliable cue for hunters, but it is unclear which cues distinguish researchers and gatherers.

5.4.4. Conclusions

Primate reactions to non-human predators are well studied, but most studies have contrasted reactions to different predator species (e.g. blue monkey *Cercopithecus mitis* reactions to simulated leopards and eagles, Papworth et al. 2008), rather than differing responses to a single species. These results suggest that hunted primates can use the behaviour of humans to distinguish between dangerous and non-dangerous individuals, and respond less strongly to lower threats. This ability reduces the potential negative impacts of antipredator behaviours on prey species. This ability is not only important when a species is frequent but attacks are not, but also when food or other resources are limited. These experiments only cover a short period after the presentation of a potential predator, but the impacts of anti-predator behaviour can be significant. Primates in hunted areas can freeze for up to five hours after encountering humans (F. Maisels, personal communication). It is worth noting that all humans had some effect on woolly monkeys, including researchers whose intentions are benign. The presence of any human could affect the behaviour of hunted primates, which may have implications for both academic research and the conservation of these species. In particular, the possible consequences of human presence and research on species, especially those threatened by hunting, should be carefully considered during the intitial stages of any project.

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Chapter 6

Non-lethal effects of hunting and other environmental factors correlated with long-term calling behaviour in the red titi monkey (*Callicebus discolor*).

6.1 INTRODUCTION

6.1.1 The non-lethal effects of human hunters on prey

The study of predator-prey interactions has a long history in ecology, but the majority of early work concentrated on the lethal effects of predators (Lima, 1998). Research on the impacts of human hunting also focuses on lethal effects; population declines due to human hunting (e.g. Peres, 2000 in Amazonia) and extent of human extraction (e.g. Fa & Brown, 2009 in African tropical forests) are well documented. Additional effects of human hunting and fishing, such as changes in phenotypic diversity (Mysterud & Bischof, 2010) and ecological cascades (such as mesopredator release; Strong & Frank, 2010) have been investigated, but these are secondary lethal effects as a result of removing individuals from the population through hunting. Non-lethal or “risk” effects of hunting, where behaviour compensates for predation risk (Cresswell, 2008; Lima, 1998), include changes in vigilance and feeding effort (Benhaiem et al., 2008), habitat selection (Creel et al., 2005; Saïd et al., 2011) and activity period (Crosmary et al., 2012). The non-lethal effects of human hunters on their prey are infrequently studied, even though humans may be the dominant predators for some species (Urbani, 2005). Non-lethal effects and their impact on populations may be more significant than lethal effects (Creel & Christianson, 2008; Preisser et al., 2005), particularly when hunting pressure is relatively light, and populations do not experience reduced density. For example, increased vigilance may mean less time is devoted to other important activities, such as feeding or social bonding. Only a small number of studies have specifically addressed the non-lethal effects of human hunting on prey behaviour, and the majority of these studies focus on ungulates and changes in habitat selection (e.g. Saïd et al., 2011; Benhaiem et al., 2008; Crosmary et al., 2012; Theuerkauf & Rouys, 2008; Brøseth & Pedersen, 2010).

Most examples of non-lethal effects of human hunting on primate behaviour are from habituated groups. In Yasuní National Park, Ecuador, habituated woolly monkeys (*Lagothrix lagotricha*) scanned the surrounding area more when they were lower in trees (Di Fiore, 2002). In Tai National Forest, Ivory Coast, (Koné 2004) found that habituated Diana monkeys (*Cercopithecus diana*) in a hunted area had fewer polyspecific associations, used higher tree strata, called and fed less frequently, and used less exposed areas of trees compared with individuals in non hunted areas. In contrast, red colobus (*Procolobus badius*) who are exposed to equal hunting pressure from humans, did not display the same behavioural changes, but rather showed more cryptic behaviours during the 3 month chimpanzee (*Pan troglodytes*) hunting season. These results could reflect differences in the dominant predator for these two species: chimpanzees for red colobus and humans for Diana monkeys.

There is some evidence of non-lethal effects of human hunting on semi-habituated primates. Watanabe (1981) studied the Mentawai snub-nosed langur (*Simias concolor*) at two sites on Siberut Island, Indonesia. He found that groups which experienced more intense hunting rarely emitted loud calls, apart from single calls when groups encountered each other in the forest at less than 20m. Groups in the hunted area also formed groups with only a single male, contrasting with polygamous groups in the lightly hunted area.

Audible signals (animal calls and the noises they make as they move though the canopy) are important for human hunters to detect prey, particularly in forested areas where visibility is low due to dense vegetation (e.g. Kuchikura, 1988). Quieter prey individuals reduce the chance of detection and therefore risk of predation. Movements through the canopy are detectable only in relatively close proximity, but long distance calls can conceivably be used by predators to locate individuals from a distance (Shultz et al., 2003). Anecdotal evidence of neotropical hunters using primate long distance calls to locate groups for hunting has been presented by several anthropologists (Urbani, 2005; de Silva et al., 2005; Hill & Hawkes, 1983). These long distance calls, however, frequently play an important role in a species social life, functioning for intergroup spacing, mate attraction and defending territories and mates (Oliveira & Ades, 2004). Reducing the frequency or duration of these calls to avoid detection by predators may change social relationships in hunted populations.

6.1.2. Red titi monkeys

Long-distance calls are the easiest way to locate red titi monkey (*Callicebus discolor*) groups (Dacier et al., 2011). These small cryptic primates live in groups consisting of pair-bonded adults and their sub-adult offspring. The adults of each group perform regular duets, which are audible from approximately 500m (Robinson, 1981) and occur in the early morning, hence have been referred to as "dawn choruses" (Moynihan 1966; Kinzey et al. 1977; Robinson 1979a; Kinzey and Becker 1983; Price and Piedade 2001; Aldrich et al. 2008). However, data from previous studies suggest that these loud calls are may be better characterised as "morning choruses", as their timing is not restricted to dawn (Table 6.1). Groups repeatedly call from the same locations and approach the territory boundary before calling, suggesting that calls are directed at neighbouring groups, rather than functioning to cement social bonds within groups (Robinson, 1979b; Kinzey & Robinson, 1983).

Calling intensity and timing may be affected by other environmental, social or physiological factors. Aldrich et al. (2008) suggested that titi monkey groups are less likely to give morning calls when it is raining and Schel & Zuberbühler (2011) demonstrated that black and white colobus monkeys (*Colobus guereza*) were less likely to give morning choruses after they had experienced a cold and wet night. As sound propagation can affect the detectability and travelling distance of calls, differences in sound propagation may affect call timing, likelihood and duration. Sound propagation decreases after sunrise as temperature rises (Larom et al., 1997), and also with increased humidity, temperature gradient and wind gustiness (Ingard, 1953). Other environmental conditions, such as the time of sunrise on observation mornings, and other sources of luminosity (in this study, moonshine) in the morning may influence the timing of choruses. Titi monkey groups do not chorus every morning, and social factors such as relationship to and recent interactions with neighbouring groups may affect the probability of calling. Studies on birds have also found that food availability and physical condition of individuals can affect the timing and probability of morning choruses (Berg et al., 2006).

Table 6.1. Results of previous studies of Callicebus species and characteristics of their morning choruses. A shaded cell indicates that the relevant information was not available. MAS = minutes after sunrise

Species	**Chorus timing**	**% mornings (number of groups)**	**Calling duration**
C. personatus	16-46 MAS[1] 1 – 302 MAS[2] dawn – 10am[3]	37.5% (1)[1] 26% and 68% (2)[3]	up to 10.5 mins[1]
C. torquatus torquatus	5.29 – 6.02am[4]	17% (1)[4]	2–7 mins[4]
Callicebus personatus nigrifrons	All day, mostly 7.00 – 11.00am (22/25 calls)[5]		28s – 12 minutes 19 seconds[5]
C. moloch	5.29-5.37am[4] 5.33-8.00am[6]		
C. moloch ornatus	As soon as it becomes light[7]		
C. oenanthe	6.30-9.30am[8]		

[1] Kinsey and Becker (1983). [2] Kimura, cited in Kinsey and Becker (1983). [3] Price and Piedade (2001). [4] Kinsey et al. (1977).[5] Martins & Silva (1998) [6] Robinson (1979). [7] Moynihan (1966). [8] Aldrich et al. (2008).

In areas where human hunters only hunt during the day, predation risk from humans will be higher during daylight hours, in areas close to communities and during hunting seasons. Previous research on habituated (Koné, 2004) and unhabituated (Kümpel et al., 2008; Watanabe, 1981) hunted primate species has found some evidence which suggests that individuals call less in areas where human hunting is more intense, in order to avoid detection by human hunters. Thus we might expect titi monkey groups to avoid detection by calling on fewer mornings in areas where hunting pressure is higher, for example, at hunted sites or in hunting seasons. Groups which call for less time may be harder to locate as there is insufficient time for hunters to move between their current location and that of the calling group. Therefore, call duration may be reduced when hunting pressure is more intense. In addition to these changes in calling intensity, timing of calls may be affected. Crosmary et al. (2012) found that three species of hunted ungulates changed their temporal niches to avoid hunting pressure, as proportionally more groups used waterholes at night. Similarly, titi monkey groups which call earlier in the morning, in particular those which stop calling before hunters start looking for prey, are less likely to experience predation.

There are two confounding factors which may differ between hunted and unhunted sites. Firstly, the acoustic habitat at these two sites may be different (e.g. density of trees, other competing sounds), causing differences in sound propagation, which may in turn, affect the timing and probability of calling. Secondly, population density may differ at hunted and unhunted locations due to hunting pressure. Although titi monkeys in the study area are not a preferred species and experience lighter hunting pressure than other primate species (Franzen, 2006), even a low hunting rate could have a profound effect on population density due to the social structure of titi monkeys. Both male and female adults contribute to infant-rearing, with the female providing milk and the male carrying infants (Fernández-Duque et al., accepted). If one adult in the group is killed, the survival of dependent offspring will be low, and in order to successfully reproduce again, the widowed adult will need to find another mate. If population density is reduced, fewer groups will occupy the same area, reducing territorial behaviours such as morning choruses (Vervust et al., 2009; Fokidis et al., 2011). A reduction in territoriality will affect calling probability and duration, but is unlikely to affect call timing.

Previous studies which suggest that primate behaviour differs with hunting pressure have focused on differences between hunted and unhunted locations, but in areas where hunting is to some degree seasonal, we may also expect behaviours to differ with temporal variation in predation risk. Nevertheless, these seasonal differences in predation pressure may be difficult to separate from other seasonal effects, such as variations in food availability or mating behaviour. This is particularly true of human hunting as human activity patterns often vary with seasons due to the availability and demands of livelihoods such as farming (e.g. Crookes et al., 2007). Although seasonal differences in behaviour can be identified in animals, it may be difficult to identify the causes of these behavioural changes if seasonal hunting correlates with other important seasonal events (Jayakody et al., 2008).

We investigate whether human hunting impacts the calling behaviour of red titi monkeys in Yasuní National Park, Ecuador, while also providing the first rigorous study determining the effects of sunrise, weather and intergroup responses on calling probability, duration and timing in this species. With increased hunting, the probability of calling and duration of calls is expected to decrease, and calling is hypothesized to occur earlier. The same changes in behaviour are also expected to occur when food is less available, which may occur in the dry season. If one site has decreased propagation, it is hypothesised that groups will call earlier, when sound travels better, and will also call more often and for longer to compensate for the reduced propagation. If densities are higher at one site, groups are hypothesized to call more often and for longer, but not change the call timing. In this study, hunting pressure is assumed higher at one site (based on information presented in previous chapters). Density and sound propagation at the two sites are measured, and seasonal differences in food availability are unmeasured. Hunting pressure and food availability are anticipated to vary seasonally, but density and sound propagation will not vary seasonally. Hypotheses are summarised in Table 6.2.

Table 6.2. Factors predicted to affect morning chorus probability, timing, and duration.

	Morning chorus characteristics		
	Probability of calling	Call timing	Call duration
Increased hunting risk	Lower	Earlier	Decreased
Decreased propagation	Higher	Earlier	Increased
Decreased density	Lower	No change	Decreased
Decreased food availability	Lower	Earlier	Decreased

6.2 METHODS

6.2.1. Study site

Data were collected in Yasuní National Park, north-east Ecuador (0°40'S, 76°24W) from January to December 2010. Yasuní National Park and the adjacent Waorani reserve cover approximately 1.6 million hectares of Amazonian rainforest. Weather is relatively constant year round, with more than 100mm of rain monthly and daytime temperatures between 22 and 34°C (Valencia et al., 2004). There is no pronounced dry season, but there are two peaks of rainfall; April-May and October-November (Derby, 2008). The area is mostly terre firme, with some seasonal flooded areas close to rivers.

Two sites close to the Tiputini River were used and all data collection was conducted on terre firme. The area around the Yasuni Research Station of Pontificia Universidad Católica del Ecuador experiences high hunting pressure from a community approximately 2km away, and from other nearby communities (Papworth et al., 2012). The Maxus Energy Corporation built a road into

Yasuní National Park in 1994, and various communities were founded along the road. Members of these communities who own canoes can easily access large parts of forest using the Tiputini River and by bus transport along the road. The majority of hunting is conducted using guns (Franzen, 2006), though traditional weapons such as blowpipes are sometimes used. All ten primate species at the site experience some degree of hunting and titi monkeys are the fifth most hunted species by number of individuals caught (Franzen, 2006). Hunters use loud titi monkey calls to locate groups for hunting (S Papworth personal observation), and only hunt during daylight (Rival, 2002; Appendix 1).

The site around the Tiputini research Station of Universidad San Francisco de Quito is approximately 26km away and only accessible by a two hour boat journey from the nearest road. This area is not thought to have been actively hunted since the station was founded in 1994, and no hunters have been observed nearby (Derby, 2008). It is impossible however, to say that there is no hunting near this station, and thus for this study it is considered to have “low hunting pressure”.

6.2.2. Apparatus

A Marantz PMD661 Professional Portable SD Field Recorder and Seinnheiser ME67 directional microphone were used to record calls. Calls were digitalised and analysed using the program Praat (Boersma et al., 2001). A Casio digital watch was used to record call times. An anchor-audio PB-25 Minivox speaker was used to broadcast a playback consisting of four repeats of a two minute duet recorded at the high hunting pressure site. The call sequence was played back so that the loudest part was at 100dB when measured at one metre from the speaker with a CEM DT-85A dB meter.

6.2.3. Sound propagation

Five locations at each site were chosen to test for differences in sound propagation of the two sites. A two minute titi monkey loud call was played using the speaker at a peak volume of 100dB. Playbacks were recorded at 10, 20 and 40m from the speaker with the microphone oriented to the speaker in all trials. Distances were measured with a 50m tape. The fourth, fifth and sixth calls of the playback were used for analysis as they had no overlapped loud calls from bird species in the recording. Two sound measures were extracted using the program Praat: median amplitude and the signal to noise ratio (SNR). SNR was calculated using the equation: $10\log_{10}(a_s - a_n/a_n)$, where a_s is the amplitude of the signal and a_n is the amplitude of background noise (from Dabelsteen 1993). Median amplitude was squared rooted to normalise before analysis. Mixed effects linear models with playback location as a random effect were used to investigate site differences in sound propagation. Amplitude and SNR should decrease with distance, and differences in sound propagation would lead to differences in the slope of this decrease at the two sites. Therefore, the interaction between site and distance was used to investigate differences in sound propagation between the low and high pressure hunting sites.

6.2.4. Observation of titi monkey morning choruses

Six unhabituated red titi monkey (*Callicebus discolor*) groups were identified at each of two sites in Yasuní National Park. Groups were initially located by sight or sound, and the number of individuals in the group was recorded on each visual encounter. Listening locations were at least 300m apart (see Figure 6.1). Titi monkeys at the study site have home ranges of approximately 0.061±0.008km^2 (Dacier et al., 2011), and were assumed not to cross some barriers such as roads and rivers, as there were no tree bridges and titi monkeys have rarely been observed to move along the ground (Lawler et al., 2006). Only loud calls were included in this study. A pilot study was used to determine titi monkey loud call times at the study site, resulting in the observation period starting at 05.00 and continuing until 08.30. Calls starting after 08.30 were not included as part of the study; loud calls which started after 08.30 were only heard six times during 13 months of fieldwork. However, calling bouts which started before 08.30 but did not end until after 08.30 were included (N=1). Data was collected on 84 mornings, with each group was visited seven times over the course of 2010 (median time between visits: 21.5 days, range 1-135) and observed from a set location which was GPS recorded. The microphone was oriented towards the focal group while they were calling. We controlled for the effect of rain on audibility and probability of calling by excluding observations from days where it rained for more than 10 minutes during the observation period.

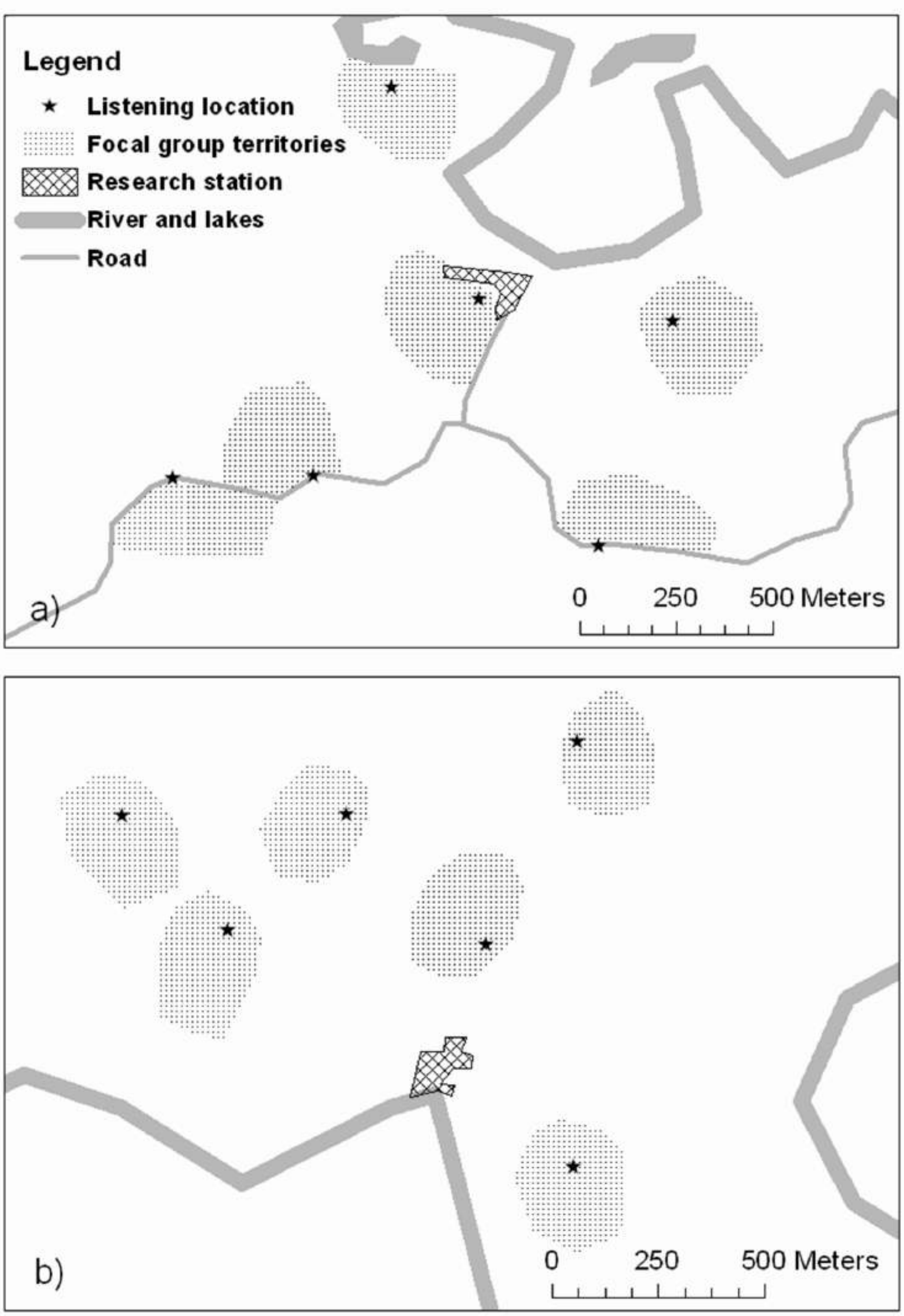

Figure 6.1.Listening locations and approximate focal group territories at a) higher hunting pressure site b) lower hunting pressure site.

6.2.5. Identification of groups and calls

As focal groups called on very few mornings, data from all audible groups, including focal groups, were used to assess the impact of human hunting pressure on the timing and duration of morning choruses. The direction, distance, start and end time of all morning chorus bouts by all groups during the observation period were recorded. A new calling bout was recorded if chorusing stopped for more than one minute. Fourty-two observation mornings occurred at each of two sites (a total of 84 observation mornings), and calling bouts were heard on 55 of these 84 mornings. On 19 mornings, all calls were heard from a single direction and distance and was assumed to be a single group. On the remaining mornings, calls were heard from various directions and distances. The number of calling groups was estimated on each observation morning, and confirmed post-hoc by mapping the distance and direction of all audible bouts for each morning.

6.2.6. Measures of calling behaviour

The probability of calling by a focal group on an observation morning and the number of audible groups on each observation morning were recorded. Three measures for each calling group on an observation morning were calculated: 1) start time relative to sunrise; 2) end time of last bout; 3) Active calling time (minutes spent calling, measured to the nearest minute for each bout). Total calling duration, from the start of the first bout, to the end of the last bout, was also considered as a potential variable, but as most morning choruses consisted of a single bout (117 of 162 morning choruses), this measure was highly correlated with active calling time. Active calling time is presented as it is the measure of calling duration more likely to vary with predation risk.

6.2.7. Predictor variables

The following variables were recorded for each observation morning:

Cloud cover; We included cloud cover as a simple measure which is correlated with both temperature and luminosity on observation mornings. Mornings were classified at the end of the observation period into one of two classes; Overcast mornings, where cloud cover was 100% throughout the observation period (n = 46 days), and non-overcast mornings, where patches of sunshine were visible on the forest floor after sunrise and cloud cover was less than 100% (n = 38 days).

Lunar phase and time of sunrise; Using data from the Astronomical Application Department of the U.S. naval observatory (http://aa.usno.navy.mil/), lunar phase and time of sunrise were calculated. Time of sunrise was defined as the time at which the upper edge of the sun's disc was on the horizon. Dawn time varied between 5.45am and 6.14am during the observation period. Lunar phase was calculated by determining the number of days to the closest full moon. As the lunar cycle is approximately 29 days, observation mornings were between one and 15 days from the full moon.

Season; Rival (2002) identified a distinct hunting season between June and August during her fieldwork with the Waorani in the 1980s, which coincided with the time when monkeys were fattest. Franzen, who studied Waorani hunters in 2002, suggested that this season starts in May (Franzen, 2006), after the peak fruiting period in April. Mornings in May, June, July and August were thus classified as the season with increased hunting pressure, and all other months as decreased hunting pressure. Information on the seasonality of plants consumed by red titi monkeys in Yasuní National Park is not available. It could be assumed that more food is available in the wetter months (April-May and October-November), and these wetter months are split between the higher and lower hunting seasons.

Number of other groups calling; As a factor which could influence calling duration, the number of other audible groups was used as a variable. When other groups are audible, titi monkeys may increase their calling time and engage in counter-calling. As an explanatory variable in models of whether focal groups called on observation mornings, only the number of groups calling before the focal group was used in analysis. If the focal group did not call, all audible groups on the observation morning were counted.

6.2.8. Population density estimates

Population densities were estimated using the methods outlined in Dacier et al. (2011). A density estimate was available from July 2007 at the site with lower hunting pressure (published in Dacier et al. 2011), so data to estimate the density of titi monkeys were only collected at the site with higher hunting pressure. Dacier et al. (2011) conducted 48 playbacks in an approximately 7km^2 area which included the area where observational data on morning choruses were collected for this study. They concluded that time of day did not affect response rate, so playbacks in this study were conducted throughout the day between 08:00 and 17:00.

68 playbacks consisting of four repeats of a two minute duet recorded at the site, with four minutes of silence between each duet, were conducted in an area of approximately 8km^2 at 250 – 500m intervals along the trail system at the higher hunting pressure site between November and December 2010. Playbacks to the 12 focal groups at distances of 15 to 100 metres were conducted to determine response rate to playbacks, and no difference was found between sites in probability of response (four out of six groups responded at each site). Playbacks were only conducted after all observational data on morning choruses at each site had been collected.

6.2.9. Analysis

The program Distance 6.0 was used to estimate density, using the hazard-rate key function with cosine adjustments. The hazard-rate model is presented as it had the lowest AICc (Aikaike's information criterion adjusted for small sample sizes) of all possible models and also allows direct comparison with the density estimates in Dacier et al. (2011),. Observations were truncated at 400m, and distances were grouped in the same bins as used by Dacier et al. (2011). Population estimates were compared between studies using the D test $\frac{mean_a - mean_b}{\sqrt{variance_a + variance_b}}$, which gives a D statistic greater than 1.96 if two population estimates are different at the 5% level (Norton-Griffiths, 1978).

All other analyses were conducted in the statistical program R (version 2.13.1, R core development team 2011). Generalized linear mixed effects models were used to determine the relative importance of each variable and to obtain averaged estimates by using model averaging and AICc weights, following Burnham & Anderson (2002). Models which better fit the data have lower AICc values, and ΔAICc for each model is derived by subtracting the AICc of the best model from the AICc of all other models. All models where ΔAICc<4 were considered, because models where ΔAICc is greater than four have considerably less support (Burnham and Anderson 2002). Model averaging is a Bayesian method and so does not produce P values, but weights across all models give the relative importance of each variable. Variable weights vary between 1.00 and 0.00; when a variable weight is 1.00, it is included in all the models within the considered model set (in this case, those models with ΔAICc<4), and when variable weight is 0.00, it is included in none of these models.

Observation location was nested within site, and so random effects for intercepts were specified in order to reflect the hierarchical nature of the data. For call characteristic measures, random intercepts were also implemented for each day of observations. Analyses were conducted in R.13.1, using the package glmmADMB 0.7.2.1 for generalised linear mixed models, and MuMIn 1.0.0 for model comparison. An interaction between site and season was included for all measures of behaviour. The AICc, ΔAICc and model weight of models where AICc<4 are reported in Appendix 5. The weights (W_i) of each variable included in the global model are reported in Table 6.3.

6.3. RESULTS

6.3.1. Population density

At the site with higher hunting pressure, density was 8.7±SE1.4 groups per km^2, with a 95% confidence interval of 6 – 12 groups, using the hazard key with two cosine adjustments. This is a lower estimate than the site with lower hunting pressure (estimate for site with lower hunting pressure from Dacier et al. 2011), 13.6±SE3.7 groups per km^2, 95% CI of 8-23 groups), but these estimates are not significantly different at the 5% level (D test: D = 0.175, p>0.05).

6.3.2. Sound propagation

For both sound to noise ratio and amplitude, the model with lowest AICc included only distance as a fixed effect (Appendix 5, weight SNR = 0.87, weight amplitude = 1.00). No effect of site was found.

6.3.3. Characteristics of morning choruses in focal groups

There was great variation in characteristics of morning choruses between focal groups (see Appendix 5). Focal groups called on just 26 of the 84 observation mornings. The number of mornings on which each group called varied between zero and five. Focal groups called on fewer mornings at the site with higher hunting pressure (nine out of 42 mornings) compared with the lower hunting pressure site (17 out of 42 mornings). The most parsimonious model to describe the probability of focal groups calling included site and cloud cover (Appendix 5). Support for this model (weight = 0.20) and these variables was moderate (Table 6.3), with the model averaged coefficients suggesting that groups at the site with higher hunting pressure were less likely to call.

6.3.4. Characteristics of morning choruses in all audible groups

Morning choruses were heard on fewer mornings at the site with higher hunting pressure (19 out of 42 mornings compared with 31 out of 42 mornings at the lower hunting pressure site), and in total 74 morning choruses were heard at the site with higher hunting pressure and 88 morning choruses heard at the site with lower hunting pressure.

The most parsimonious model explaining how many groups were audible on observation mornings included a single variable, hunting season (Appendix 5, weight = 0.52), with fewer groups calling during the season with higher hunting pressure. Season was also the most important variable across all models and support for differences with site, cloud cover and the interaction between site and season was low (Table 6.3).

Groups started calling between 05.05 and 08.22am (median = 6.10am, n=162). Initial analyses indicated that sunrise was an important factor influencing start time, with calling starting later when sunrise was later. Therefore, start time relative to sunrise was used for analyses. Calls occurred both before and after sunrise (median = 17 minutes after sunrise, range = 42 minutes before sunrise to 157 minutes after sunrise, n = 162). The most parsimonious model for calling (Appendix 5, weight = 0.35). The most important variables across all models were season and site,

Table 6.3. Variable weights (W_i) from all models where AICc<4 for each measure of morning choruses. Random effects, sample size and test distribution are displayed. Grey boxes indicate a fixed variable was not included in the global model. Variance explained by the random effects is included where appropriate. Fixed effects whose weight in the averaged models was greater than 0.60 are indicated in bold. Probability of focal groups calling (N=84). Number of audible groups (N = 84). All other variables (N=162).

Response	**Site**	**Season (Hunting, Not hunting)**	**Season x Site**	**Weather (overcast, non-overcast)**	**Number of groups calling before focal group**	**Number of groups calling**	**Lunar phase (full, new)**	**Random effect: Group nested in site**	**Random effect: Observation Day**
Focal group called	**0.66**	0.21	0.05	0.51	0.20			x	
Number of audible groups	0.27	**1.00**	0.00	0.29				x	
Start (mins from sunrise)	**0.91**	**1.00**	0.59	0.19			0.19	x	x
End (mins after observation start)	**0.86**	**1.00**	**0.74**	0.26				x	x
Active calling time (mins)	0.59	**0.70**	0.49	0.26		0.26		x	x

start time relative to sunrise included hunting season, site and an interaction between the two with less support for an interaction between season and site and little support for the influence of cloud cover, or the lunar cycle (Table 6.3). Groups called latest at the low hunting pressure site in the decreased hunting season, and earlier at the same site in the increased hunting season and at the high hunting pressure site (Figure 6.2a).

Of the morning choruses heard during the study, 117 of 162 consisted of a single bout (range 1 to 9 bouts, n=162). Median time spent actively calling ranged between one and 37 minutes (median = 4 minutes, range = 162, all measurements rounded up to the nearest minute). The best model for active calling time also included season, site and an interaction between season and site (Appendix 5, weight = 0.22). Time spent actively calling was similar for both seasons at the site with higher hunting pressure, but at the site with lower hunting pressure active calling time was lower during the season with increased hunting pressure (Figure 6.2b)

Groups stopped calling between 05.13 and 08.39am (median = 6.40am, n=162). The most parsimonious model included season, site and their interaction (Appendix 5, weight = 0.48). Across all models, the most important variable was season, followed by site and the interaction between site and season (Table 6.3). Little evidence was found for the importance of cloud cover. At the site with higher hunting pressure, end time did not differ with season; in both seasons groups finished calling at a time intermediate between the decreased and increased hunting seasons in the low hunting pressure site (Figure 6.2c). In general, calling times at the lower hunting pressure site showed a shift to earlier call times when hunting pressure was greatest. In contrast, little difference in timing was found at the site with higher hunting pressure, but the probability of hearing a group call at any time was lower.

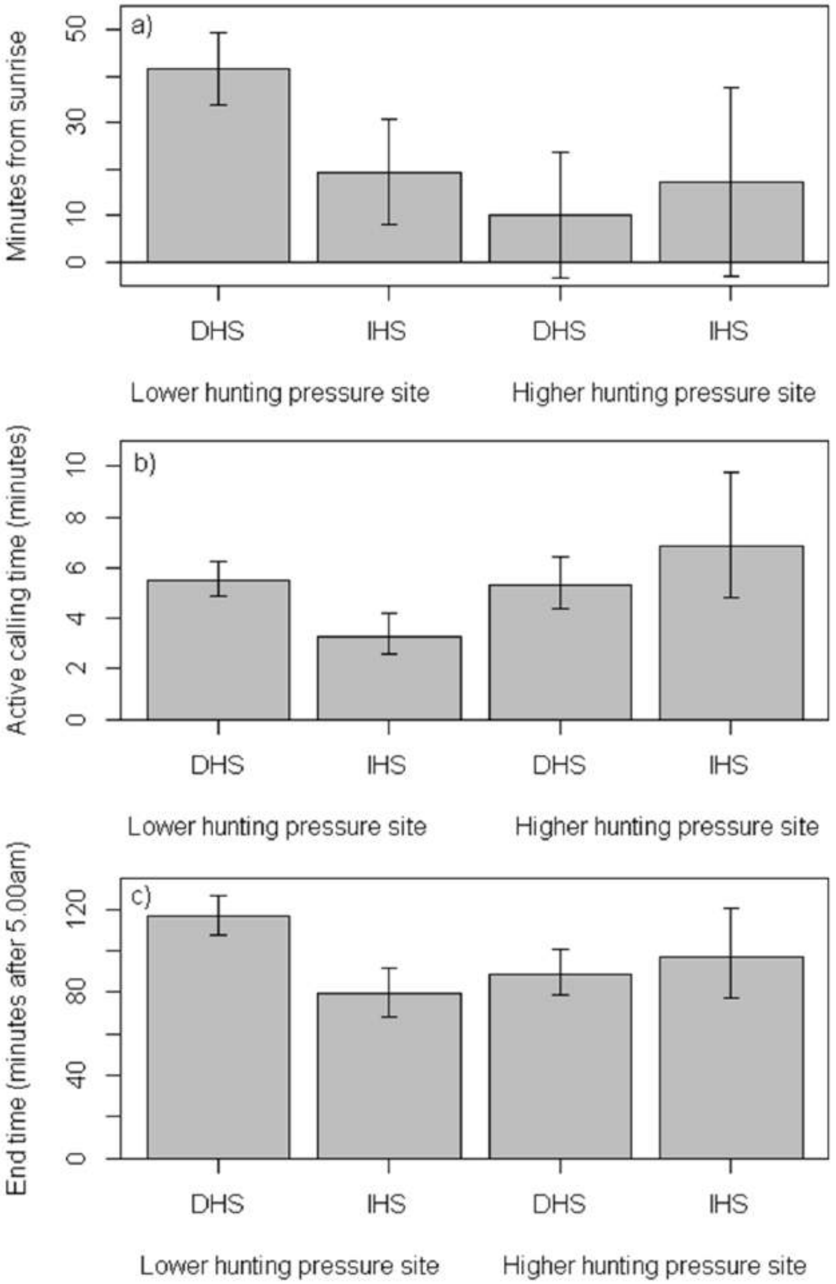

Figure 6.2. Model coefficients and standard errors from best (lowest AICc) model of a) Start time of morning choruses relative to sunrise; b) Active calling time in minutes; c) End time of morning choruses in minutes after 5.00am. DHS = Decreased hunting season, IHS = increased hunting season.

6.4. DISCUSSION

6.4.1. Non-lethal effects of human hunting on titi monkey morning choruses

No differences in sound propagation, measured by sound-to-noise ratio and amplitude, were found between the two sites. This may be because the two areas are just 26km apart and have similar tree species, topography and provide similar acoustic habitats. Although the estimate for titi monkey density at the high hunting pressure site was lower, it was not significantly different from densities at the site with lower hunting pressure. The census at the low hunting pressure site was conducted three years before the present study, but if human hunting was reducing densities at the site with higher hunting pressure, we would expect the difference between the two sites to be exacerbated, increasing the chance of a false positive. A previous study of primate densities in the Amazon found no evidence of competitive release in small primates (including *Callicebus* spp.) when larger species are hunted (Peres & Dolman, 2000), so it is unlikely that competitor release at the hunted site is compensating for hunter offtake. Thus it appears that human hunting is not having a significant impact on population densities of titi monkeys at the site with higher hunting pressure. This may be because titi monkeys are comparatively lightly hunted at the site where hunting pressure is highest (when compared with other primate species, Franzen, 2006), so offtake does not affect group densities. However, this study compares two areas, rather than a single area at two different periods, and it is unknown how other factors which differ between the sites may affect density. To confirm that human hunting is not reducing densities, a future census at the same location would be necessary, as other factors relevant to titi monkey population density may differ between the two sites.

In previous studies, density has been shown to affect the behaviour of territorial species by changing the intensity of interactions (Vervust et al., 2009). Although the density estimates given in this paper seem high compared with density estimates from line transects in other areas, it is not possible to make direct comparisons due to the differing methodologies used, as Dacier et al. (2011) explain. Line transects used at other sites are likely to underestimate *Callicebus* densities due to their cryptic behaviour, and the densities estimated using the playback method are consistent with density estimates based on home range size (Dacier et al., 2011). It is not possible to make conclusions about any specific factors which may or may not be influencing density at these two sites, but as the densities are similar, differences in call characteristics can be potentially attributed to other differences between sites, such as hunting pressure, rather than differences in territorial behaviours because of population density.

In addition to not finding significant differences in density and sound propagation, the site differences in call characteristics are consistent with the hypothesis that hunting pressure is altering call characteristics (Table 6.2). Focal groups at the higher hunting pressure site were less likely to call, and at both sites more groups were heard during the season with decreased hunting pressure. It is possible that these differences in call characteristics are a result of other, unmeasured, differences between the sites and seasons, such as food availability. Without knowing if titi monkeys at Yasuní National Park experience seasonal shortages of food, it is difficult to determine whether these seasonal differences are a result of hunting pressure.

Seasonal differences in call timing and duration were found at the site with lower hunting pressure, whereas no seasonal differences were found at the site with higher hunting pressure. This pattern of behaviour is consistent with the predictions of the predation risk allocation hypotheses (Lima & Bednekoff, 1999). This hypothesis predicts that greatest anti-predator behaviour will be displayed when high-risk situations are brief and infrequent. Although originally developed to explain time trade-offs between feeding and vigilance, prey animals also trade off predation risk with other essential behaviours such as territory defence (Lima, 1998). Prey behaviour conforming to the expectations of the predation risk allocation hypothesis has been previously demonstrated (Ferrari et al., 2009), but this is the first time this pattern has been observed as a response to predation risk from humans.

6.4.2. Additional factors affecting morning choruses

In addition to the effects of hunting, other environmental factors had some influence on morning choruses. Time of sunrise had a strong positive effect on start time of morning choruses, though groups showed great variation in start time, starting both before and after sunrise. In general, cloud cover had little effect on call characteristics. Little effect was also found for lunar phase. Moonlit nights do provide greater illumination, which could affect starting time of morning choruses, but light from the moon appears insufficient to prompt earlier calling times. Social factors, as measured by the number of other groups calling on observation mornings, also had little effect on call characteristics. As morning choruses in titi monkeys are thought to function in territory defence, it is interesting that this social factor had little effect. Past territorial challenges (as found by Armrhein & Erne, 2006) and relationships between groups may be more relevant measures of titi monkey social interactions than the simple measure of how many other groups call used in this study.

6.4.3. Implications for animal behaviour and conservation

Non-lethal effects of human hunting can occur in species which are only lightly hunted, and these effects can have substantial impacts on the social interactions of individuals. In this study, non-lethal effects of hunting were found to have a measurable impact on call characteristics, whereas there was no significant difference in population sizes, which may have indicated lethal effects. Individual level non-lethal effects can scale up to population level effects, such as the observed differences in call timing, duration and probability in this study.

There are practical implications of this information, both for the study of animal behaviour and conservation. Aldrich et al. (2008) used observations of morning choruses to census Andean titi monkeys, but used published call rates of other species in their calculations to determine population size. If calling rate can be suppressed by human actions such as hunting, then population size in disturbed populations such as studied by Aldrich and colleagues could be seriously underestimated. Probability of calling should be determined for a study population before using the method of Aldrich et al. (2008), or alternately, the playback method of this study could be used. The differences between the two sites in this study also raise questions about our ability to predict species behaviour from observations at single sites. Many animal behaviour studies draw species-level conclusions about behaviour from observations at a single site. This study suggests that it may be difficult to predict behaviours between sites even at a very localised scale.

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Chapter 7

Synthesis and implications for conservation

Conservation has moved a long way from the guns and fences approach, which excluded people from areas with the aim of protecting the natural environment (Crane et al. 2009). Recent research has highlighted the importance of integrating humans and human behaviour into conservation research and understanding how humans interact with the environment (Kümpel et al. 2009; Van Vliet et al. 2010). In this dissertation, I explored hunter-prey behavioural interactions in a single system, examining human perceptions of their prey and human forest behaviour, and the short and long term effects of hunting on primate behaviour.

7.1 IMPLICATIONS OF RESULTS FOR FUTURE RESEARCH

7.1.1 Waorani perceptions of primates

Local ecological knowledge (LEK) is often used in conservation projects to gain information about the ecology or management of certain species. LEK can also help the researcher understand the cultural context of research, particularly when this research focuses on human behaviour. Previous research suggested that primate species are important in Waorani culture (Rival 2002). I interviewed 35 Waorani participants, using free listing, photographs, and pile sorting to investigate Waorani perceptions of primates and other mammals. I showed that woolly monkeys (*Lagothrix poeppigii*) clearly play a significant part in the culture of the Waorani, but the special place of woolly monkeys in Waorani society could not be extended to all primates. The research also highlighted the importance of some non-primates species, in particular the white-lipped peccary (*Tayassu pecari*). In general, the cultural saliency of mammals was correlated with their contribution to the diet of the communities, and white-lipped peccary was the favoured species and was most consumed. Questions on focal species identified three species which had not been previously recorded as consumed by the Waorani. One of these species, the tayra (*Eira barbara*), although never mentioned in free lists, was the species most frequently perceived as a crop raider, highlighting the valuable contributions of social science methods such as interviews for conservation science. Chapter three also highlighted the emic nature of LEK, and cautioned those using LEK that such information is intrinsically cultural and subjective.

When ethnoprimatology was highlighted as an important area for study, the Waorani were suggested as a starting point due to the importance of primates in Waorani diets (Sponsel 1997). This study demonstrated that in the studied Waorani communities, there is a correlation between dietary importance and cultural importance. I also highlighted however, that although received knowledge appeared to be correct in stating that woolly monkeys are important (Rival 2002), this importance could not be generalised to all primates. Previous ethnoprimatological studies in the lowland neotropics were consistent with this study in finding evidence that olingos and kinkajous are considered types of primates (Lizarralde 2002; Urbani 2006). In future studies in ethnoprimatology in which participant definition of “primate” differs from that of the researcher, researchers should consider if they wish to present researcher or participant defined “ethnoprimatology”.

These results suggest that ethnoprimatological studies should be cautious in focusing their attention on only primates when investigating a particular culture. Ethnoprimatology is based on the researcher’s prior assessment of primate importance in a given culture, but this assumption should be tested for each studied culture, particularly given the stated aim of ethnoprimatology to inform conservation (Riley 2006). In the case of the Waorani, the white-lipped peccary was both the preferred species for consumption, and also contributed most to Waorani diets, so understanding their relationship with the Waorani could contribute to future conservation projects. As peccary move over large distances (Fragoso 1998), their anti-predation strategies may involve avoidance of areas with higher human hunting pressure rather than behavioural modifications in areas where hunters are present. This could have implications for forest structure as peccary disperse the seeds of many plant species which are eaten by the Waorani (Beck 2006).

Chapter three also highlighted the relationship between human natural resource use and perceptions of the natural environment. Waorani perceptions of animal diets and the cultural salience of mammals both showed strong correlations with patterns of consumption in the communities. Those using LEK sometimes assume that objective truth can be extracted from LEK, and so attempt to validate LEK using western scientific knowledge (e.g. Rist et al. 2010). LEK which cannot be validated in this way may be discarded. Comparison of LEK and western scientific knowledge as a mutual exercise designed to exchange knowledge from local people and outside observers, is likely to better support conservation projects, as new perspectives can be gained by both parties. This approach allows greater involvement of local knowledge holders and may increase support and interest in any conservation project (Nelson 2005).

7.1.2. Hunter movement ecology and habitat selection

Understanding patterns of resource extraction is crucial for conservation science, allowing accurate assessments of system sustainability and testing key assumptions about human resource use. I applied ecological methods and principles to Global Positioning System (GPS) data on human movement to investigate the ecological and behavioural differences between human hunters and non-hunters. The integration of movement ecology and habitat selection can greatly augment the applicability and scope of both disciplines, and I explored the issues that arise from integration, due to the differing data types and methods used by each approach. I developed a methodology which integrated movement ecology and habitat selection of human hunters, and can be used on any species which routinely return to a central place.

Spatial models of human hunting in the tropics have usually relied on forest types or other zoning methods to distinguish areas with different hunting pressures (e.g. Parry et al. 2009; Sirén et al. 2004). I demonstrated that Waorani hunters do not conform to the traditional model of hunter space use. Rather hunters tended to repeatedly use some areas, and leave other areas untouched, potentially creating microrefugia in a hunted landscape. Although sink-source dynamics in human hunting have well developed theory (Hill and Padwe 2000), relating this theory to a practical understanding of species management requires greater understanding of where source and sink areas are located in the spatial and temporal landscape. The methods outlined in this thesis can identify hunted and unhunted areas, which could be used with information on species behaviour, such as territory size, to determine the probability that unhunted areas could support viable populations of hunted species.

The results of chapter four suggest that habitat selection may be an important tool in describing and predicting hunter behaviour. This study however, only used these methods to describe hunting pressure. The methodology certainly has the potential to allow predictions of hunter behaviour, but this needs to be empirically tested before the methodology and habitat selection and the outlined methodology is widely adopted in conservation. Furthermore, the methods described are specific to active hunting methods, such as gun and blowpipe hunting. In the study area, trapping methods were not used, but they are widely used in other areas (e.g. Kümpel et al. 2009). As traps are stationary, it is not possible to describe their movement with net squared displacement (NSD). Likewise, the biased random bridge (BRB) method of constructing a utilization distribution, which assumes movement between successive points, is not appropriate. Alternate methods for constructing a utilization distribution would need to be adopted in the methodological framework I outline before it was appropriate for investigating trap hunting.

7.1.3 Primate anti-predator responses to humans

The different behaviours of hunters and non-hunters, not only in the tools they carry, but also their speed and use of space, may allow prey to distinguish between dangerous and non-dangerous individuals and react appropriately. Quantifying these differences using the methodological framework outlined in chapter four provided justification for the experiments described in chapter five. Only responding to threatening individuals allows prey species to minimise energy expenditure and other costs of predator avoidance, such as disruption of feeding. This effect is termed the threat sensitive predator response hypothesis (Helfman 1989). If hunted animals are unable to distinguish dangerous humans from non-dangerous humans, human hunting is likely to have a greater effect on prey populations as all human encounters should lead to predator avoidance, potentially increasing stress and creating other costs for exploited populations (Monclús et al. 2009). Variation in anti-predator responses to humans within a single species had previously been observed in primates (Zuberbühler et al. 1997; Zuberbühler 2000; Arnold et al. 2008), although received wisdom suggested that freezing was the most appropriate response to human hunters (Zuberbühler 2007). I conducted experiments on Poeppigi's woolly monkeys (*Lagothrix poeppigii*) as they were identified as the preferred, and most consumed, primate species for the Waorani in chapter three. Groups of woolly monkeys were presented with human models engaging in one of three behaviours "hunting", "gathering" or "researching". These experiments were conducted at two sites with differing hunting pressures. Visibility, movement and calling were recorded, and showed that groups changed their behaviours after being exposed to humans, and did so in different ways depending on the behaviour of the human model. These results support the hypothesis that the general primate response to human hunters is freezing, but also suggest that primates may distinguish different human behaviours. Results at the site with higher hunting pressure were consistent with predictions based on the threat sensitive predator response hypothesis.

Previous experiments where humans were presented showed inconsistent primate responses (e.g. Arnold et al. 2008). This study suggests a possible explanation for this variation, as the study groups may have responded differently to human models behaving in different ways. These effects may not be limited to only primates, and the effect of human behaviour and the interactions with the behaviour of other hunted species is an area for further study. If a species antipredator response to humans is understood, playbacks and predator model experiments could be used by conservation practitioners to map prey perceptions of the landscape of fear. Differences in behaviour between hunted and unhunted areas could be exploited by investigators to provide rough-and-ready estimates of hunting pressure in an area. This could be of particular use where local people are unwilling to discuss their hunting behaviour due to taboos, stigmas or illegality, or when investigators wish to determine where to focus their efforts. Using playbacks, Bshary (2001) found that monkeys in hunted areas were able to distinguish eagle calls from hunter imitations of eagle calls; whereas they called to warn other individuals of the "real eagle", they remained silent when hunter eagle imitations were played. In contrast, monkeys in unhunted areas were unable to make this distinction and called as if an eagle were present to both playbacks. For each species, differences in behaviour between hunted and unhunted areas would have to be quantified before this method is practically applicable for conservation.

7.1.4. Long term effects of human hunting on primate behaviour

Previous research suggests that primates may show long-term behavioural differences in areas where they are hunted, but this research has been conducted on observations of habituated (Koné 2004) or semi-habituated groups (Watanabe 1981) and the effect of human observers on these behaviours has not been quantified. Titi monkeys (*Callicebus spp.*) are found throughout South America, and all species engage in loud morning choruses. In areas where titi monkeys are hunted by humans, these loud calls are the easiest way to locate and hunt groups. Groups which chorus less or earlier may reduce predation risk from human hunters. I investigated the impact of human hunting on the loud calls of red titi monkeys (*Callicebus discolor*) at both a high and low hunting pressure site. Titi monkey densities as estimated using a playback census method were not significantly different at the two sites. Observations of 162 choruses on 84 mornings were consistent with expected effects of human hunting pressure, as groups were less likely to call and called earlier in areas of higher hunting pressure. In addition to demonstrating the non-lethal effects of human hunting, these results have wider implications for conservation and primatology: density estimates based on observations of spontaneous primate calls may not be directly comparable between sites with different levels of human disturbance due to different calling rates, and observations at a single site may not represent species level behaviour.

In chapters five and six I demonstrate that hunting pressure and human presence is associated with reductions in behaviours such as calling, which hunters and researchers use to locate individuals. Species red-listing and some sustainability indices rely on estimates of species density, but these estimates can be biased by animal behaviour (Buckland et al. 2001; Kümpel et al. 2008). In particular, primate censuses rely on visually identifying groups and estimating the distance between the observer and the group centre (Buckland et al. 2010). If the behaviour of primates in hunted areas makes them less obvious to observers, the probability of undercounting will be higher than in areas where they are not hunted. This difference in behaviour will result in lower density estimates in locations with hunting compared to unhunted areas, increasing the chance of a type I error. Densities in hunted areas are expected to reduce, and this bias may increase the difference in density estimates between hunted and unhunted sites. This effect may cause researchers to conclude that there are density differences when none are present, leading to ineffective allocation of conservation resources. This undercounting in density estimations also has implications for sustainability indices which incorporate some measure of population size or density (e.g. Robinson and Redford 1994). In this case, the reduced density estimate (compared with what is actually present in the area), will increase the probability that extraction of a particular species is declared unsustainable. As many people rely on wildmeat as a source of protein (Milner-Gulland and Bennett 2003), introducing conservation measures to reduce hunting which has been mistakenly identified as unsustainable could have undesirable consequences. Observer effects on the accuracy of primate population estimates, and how they vary spatially, has not been quantified, but is an important area for future study.

These observer effects on detection in censuses could be overcome if alternate methods are used. Observational auditory census methods have been previously used for primate species with loud calls, such as howler (*Alouatta spp*) and titi monkeys (Estrada et al. 2004; Aldrich et al. 2008). These methods however, are also likely to result in the same biases if species reduce their calling in hunted areas, such as the reductions in calling observed in titi monkeys in this study. The playback method used in this thesis offers an alternate and effective way to measure the density of hunted populations. Many primate species have loud calls, and numerous species have also been shown to respond to playbacks of conspecifics and other species (e.g. Papworth et al. 2008; Herbinger et al. 2009). Although hunted species should theoretically respond to conspecific playbacks, this would need to be verified on a species-by-species level, and it would be necessary to demonstrate that species always respond at zero distance in both hunted and unhunted areas before the method could be widely applied.

7.2 CONCLUSIONS

Humans are part of the natural environment, and integral to the discipline of conservation biology. Thus understanding the behaviour of humans and the other organisms they interact with can help conservation. Hunting, particularly in the tropics, has received much attention in conservation biology, but some aspects of the behaviour of both hunters and their prey are poorly understood. This dissertation represents the first detailed evaluation of human hunting behaviour and primate responses as human prey in a single system. Methods and theory from diverse disciplines were used to investigate Waorani hunting and their perceptions of prey, as well as the behavioural responses to Waorani hunters by some of these prey animals. The implications of the results are also discussed, and areas for future study suggested. The value of integrated studies of human and animal behaviour in conservation biology is highlighted, and also some of the issues which may arise from working in multiple disciplines. Continuing research on human and animal behaviour will aid conservation by providing greater understanding of the systems in which conservation efforts take place. Integrated studies of human and animal behaviour are not always straightforward. If conservation biology is to continue working in a variety of disciplines and adopting new methods and theories, integrating these disciplines and understanding the differences between them is vital.

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Appendix 1

Additional general information on current Waorani hunting

This appendix contains information collected using the methods outlined in chapters three and four, but which was not included as part of these chapters.

A1.1 Contemporary hunting methods

Twenty-nine individuals at the study site answered questions about their hunting behaviour and animal use. For a summary of the methodology and the age/sex structure of participants, please see the methods section of chapter three. Individuals were asked if they had ever hunted with a blowpipe or gun, which they preferred (if they had used both), and whether women hunted.

Nineteen of 29 individuals stated they had hunted at some point in their life. Three had only used machete, dogs or spears to hunt. Twelve individuals had used a blowpipe, and 11 individuals had used a gun. Individuals who preferred to use guns stated that blowpipes were too heavy, or too difficult, and with a gun you could immediately see if you were successful, rather than waiting for the curare poison to kill the target. Those who preferred blowpipes stated that guns made too much noise and scared animals away, or that gun cartridges were too expensive. Blowpipes were considered particularly effective for monkey species, as more than one individual could be shot before the others realised the hunter was present. Using lances to kill peccary was generally considered difficult and requiring skill, as the lance has approximately a five meter range and the peccaries frequently ran past and escaped. Individuals also reported seeing certain animals and deciding not to hunt them. They gave various reasons for this, but most either stated that they were leaving this group or species for a later hunting trip, or they were already tracking another species, such as white-lipped peccary. Many individuals reported hunting smaller species, such as the golden-mantled tamarin and small birds, when they were younger to practice using the blowpipe. Most individuals recounted sharing of meat between family members in different households. Individuals who stated they had never hunted (n=10) were all female.

Of the 19 individuals who stated they hunted, five were female. Women who had hunted usually did so opportunistically, killing animals with a machete or dogs when they encountered them in their fields. Sixteen individuals were specifically asked if women hunted and were exactly divided, with half replying yes, and half replying no. Those who replied that women did hunt stated that this was occasional, unusual, or had occurred more in the past. Although women did not actively hunt, many stated that they told their husbands where they found game species whilst in the forest, and sometimes returned to the forest to accompany their husbands to these locations. In one successful hunt, a woman saw woolly monkeys with infants, and wanted one as a pet. She returned to the community to tell her husband, who went to the area and caught a female with infant. The female was eaten, and the infant kept as a pet. On another occasion, two women were going to collect domesticated plants from a forest clearing when they encountered a group of white-lipped peccary. They returned to the community and all the men returned to the area to hunt the peccary.

Various taboos were mentioned during conversations with individuals, although some were personal or temporal, rather than prescriptive. Both spider monkeys and saki monkeys were mentioned as species which should not be eaten by pregnant women, with one individual stating that the child will be thin if this happens. Saki monkeys were said to make people ill, as were spider monkeys and the tayra, which gave some individuals headaches and made them feel dizzy. Capuchin monkeys made some individuals tremble. Other individuals also stated they did not like howler monkey, as they had a lot of worms in the meat and tasted bad, but others mentioned howler monkeys as one of their favourite meats, suggesting that this was a preference, rather than a taboo.

A1.2 Non-consumption uses of primates and other animals

Woolly monkeys, spider monkeys, owl monkeys, pygmy marmosets, collared peccary and numerous birds, including *Ara* and *Amazona* species, were observed as pets in the communities. During interviews, at least one individual stated that they or a family member had kept each focal species as a pet. Golden-mantled tamarins were reported as the preferred species for pets, as they were clean and ate cockroaches, but the most commonly reported pet was the woolly monkey. The tails of saki monkeys, squirrel monkeys and the kinkajou were all reported to be used to decorate traditional crowns. Bird feathers were also used frequently used as decoration, such as the use of *Ara* spp. feathers on hunting spears.

A1.3 Forest trips

Participants were approached to carry a GPS during forest trips, and answer short questionnaires before and after the trip. One Waorani assistant was employed in each community to administer questionnaires. This allowed data to be collected from more than one community at once, though the majority of data was collected from Timpoca, the community closest to the area in which monkey behaviour was studied. The assistant was responsible for the GPS unit when not in use, asking questions of participants before and after their forest trip and explaining the use of the GPS to new users. All adult males which permanently resided in Timpoca contributed at least one trip to the data set, and visiting individuals were invited to participate. Only three females participated in the study, though numerous attempts were made to increase female participation. The questionnaire was translated from English to Spanish with the aid of 3 bilinguists. These questions were then validated with the Waorani assistants for clarity and meaning, before being translated back to English by two different bilinguists. Before leaving, the participants were asked the following questions (translated from Spanish):

1. Why are you going to enter the forest?
2. Which tools are you taking?

On their return from the forest, participants were asked the following questions (translated from Spanish):

1. What monkeys have you seen?
2. Have you brought anything out of the forest that you didn't take in?

A total of 89 trips were recorded and 26 reasons were given for forest trips. The most commonly stated purpose of a hunting trip was "hunting for food", followed by "hunting for animals for food" (Table A1.1). Individuals carried a machete on almost all trips, and the second most commonly carried item was a gun, followed by fishing tackle (Table A1.1). Blowpipes and dogs were taken on five and four trips respectively. The typical trip starts at 8.30 am (median, range: 5:30am – 16.55pm, n = 88), with three people (median, range: 1 -11 people, n=89) and lasts five hours and 28 minutes (median, range 46 minutes to 10 hours and 10 minutes, n=61). 77 of 89 trips returned with something from the forest, most frequently with fish (33 trips).On four occasions, monkeys were caught and returned to the village (Table A1.2). Monkeys were seen on the majority of trips (79 of 89 trips), and the most frequently seen species was the woolly monkey (39 trips) (Table A1.3).

Table A1.1. Stated trip purpose with equipment taken on trip and products brought back from the forest.

Reasons for going to the forest	**Number of trips**	**Equipment taken on trip**		**Products brought from the forest to the village**				
		Gun or blowpipe	Fishing gear	Meat	Fish	Other	Nothing	NA
Hunting to get food	19	9	10	9	10			
Hunting to get animals for food	15	13	2	13	2			
Fish to get food	7		7		7			
Search for animals	7	2	1		1		4	2
Search for food	5	3	3		2	2	1	
Hunting for food	4	4		3				1
Fish	3		3		3			
Hunt	3	2		1				2
To watch	3						3	
Animals	2	1					1	1
Catch animals	2	1				1	1	
Hunting	2	2		1			1	
Hunting animals	2	1		1			1	
To see animals	2	2		1	1			
To see monkeys	2					1	1	
Get barbusco (a type of fish)	1				1			
Get cöhuañe (red brocket deer, *Mazama amerciana*)	1	1	1		1			
Get morete (*Mauritia flexuosa)*	1				1			
Hunt animals	1	1			1			
Hunt to get food	1		1		1			
Hunting and fishing	1	1	1		1			
Hunting and getting food	1	1			1			
get food	1	1		1				
The animals miimo (Golden-mantled tamarin, *Saguinus tripartitus*)	1	1		1				
To plant	1	1				1		
To watch monkeys	1						1	
Total	**89**	**47**	**29**	**31**	**33**	**5**	**14**	**6**

Table A1.2. Items brought from the forest

Item	Species	Number of trips
Fish	Various	33
Nothing		14
Collared peccary	*Pecari tajacu*	8
Paujil	*Crax spp.*	5
Tapir	*Tapirus terrestris*	4
White-lipped peccary	*Tayassu pecari*	4
Spider monkey	*Ateles belzebuth*	2
Tortoise	Various	2
Howler monkey	*Alouatta seniculus*	2
Macaw	*Ara spp.*	1
Deer	*Mazama spp.*	1
Paca	*Agouti paca*	1
Black agouti	*Dasyproctes fuliginosa*	1
Crops	Various	2
Palm grubs	*Rhynchophorus spp.*	1
Wild cinnamon	Unknown	1
Chambira palm	*Astrocaryum chambira*	1
Item not specified		5
No data		1

Table A1.3. Number of trips in which each monkey species was seen, and their reported densities where available.

Common name	Scientific name	Number of trips seen	Reported density, individuals/km^2 *	Difference in rank of seeing and density rank
Poeppigi's woolly monkey	*Lagothrix poeppigii*	39	20.4	+1
White-fronted capuchin monkey	*Cebus albifrons*	23	7.97	+3
Golden-mantled tamarin	*Saguinus tripartitus*	22	18.75	0
Common squirrel monkey	*Saimiri sciureus*	14	32.75	-3
White-bellied spider monkey	*Ateles belzebuth*	12	6.75	+1
Red howler monkey	*Alouatta seniculus*	12	5	+2
Equatorial saki monkey	*Pithecia aequatorialis*	10		
Pygmy marmoset	*Cebuella pygmaea*	2		
Noisy night monkey	*Aotus vociferans*	1		
Red titi monkey	*Callicebus discolor*	1	9.69	-3

*Data taken from Derby (2008). Census conducted in 2005 approximately 20km from community in which hunting was studied, and within an area in which the community occasionally hunted.

Appendix 2

Additional information on focal species and summary of primate studies referred to in chapter three. Wild plants consumed by the Waorani and AICc for models of cultural saliency.

Table A2.1. Focal species used for species identification and pile sorting. The rate of extraction in kg and number of individuals by the communities during 5 months (from Franzen, 2006) for each of these species is also shown. Species names follow the IUCN redlist (accessed online 19th June 2012) for both scientific and common names. Primate species are shown in bold.

Scientific name	Common name	Name in Wao terero	Other names used by interviewees	Weight extracted (kg)	Number of individuals extracted	Individuals traded at Pompeya market
Tasyassu pecari	White-lipped peccary	Urè	Guangana, pecari de labios blancos	2726	106	391
Lagothrix poeppigii	Poeppig's woolly monkey	Gata	Chorongo, mono, mono lanudo, monkey	471	83	61
Ateles belzebuth	White-bellied spider monkey	Deye	Maquisapa, mono araña, araña	453	58	9
Pecari tajacu	Collared peccary	Amo	Sajino, pecari de collar	567	28	97
Alouatta seniculus	Colombian red howler monkey	Iwa	Aullador, cotomono, mono colorado	161	28	1
Mazama americana	Red brocket deer	Cöhuañe	Venado	366	19	49
Cebus albifrons	White-fronted capuchin	Bogi	Machin, mono machin, capuchin	52	18	2
Callicebus discolor	Red titi monkey	Gänaroca	Songosongo, mono titi, cotoncillo	7	10	1
Pithecia aequatorialis	Equatorial saki monkey	Cuwïncu	Parahuaco, mono saki,	21	8	0
Saimiri sciureus	Common squirrel monkey	Gekirè	Bariso, mono ardilla, ardilla	4	4	3
Tapirus terrestris	Lowland Tapir	Titë	Danta, tapir	352	3	14
Aotus vociferans	Noisy night monkey	Amönka	Mono nocturne	1	3	0
Eira barbara	Tayra	Öcata	Cabeza de mate	11	2	0
Saguinus tripartitus	Golden-mantled tamarin	Mimö	Chichico, tamarino	1	2	1
Hydrochaeris hydrochaeris	Capybara	Tota	Capybara	34	1	8
Potus flavus	Kinkajou	Gamönga	Ganata, cusumbo	2	1	0
Cebuella pygmaea	Pygmy marmoset	Gatomo	Leoncillo, mono de bolsillo	0	0	2
Bassaricyon alleni	Allen's olingo	Ganata	Gamönga, tutamono	0	0	0

Table A2.2. Summary of studies used to determine the diet of four primate species

Study	Study species	Study location	Study length	Methodology	Data presented
Carrillo-Bilbao et al. (2005).	*Callicebus discolor*	Yasuní National Park (74°30'W, 0°42'S)	260 hours	Focal samples	All species consumed
Dew (2005)	*Lagothrix poeppigii, Ateles belzebeth*	Yasuní National Park (75°28'W, 0°42'S)	*Lagothrix*: 429.45 hours; *Ateles*: 457.45 hours	Focal samples	Fruit consumed – identified to genus. Occasionally identified to species
Di Fiore (1997)	*Lagothrix poeppigii*	Yasuní National Park (75°28'W, 0°42'S)	690 hours	Scan and focal samples	Genus contributing >1% of diet
Kostrub (2003)	*Saguinus tripartitus*	Tiputini Biodiversity Station (76°20'W, 0°40'S)	146 days	All occurrence	All species consumed
Suarez (2006)	*Ateles belzebeth*	Yasuní National Park (75°28'W, 0°42'S)	1268 hours	Focal samples	All species consumed

Table A2.3. Wild plants reported eaten by the Waorani, and consumption of these genus' by four primate species in Yasuní National Park. Same species consumed (S); same genus consumed (G).

				Species which consumed the same genus			
Name (Wao terero)	Scientific name	Number of families which reported eating species	Number of days species eaten	Spider monkey*	Woolly monkey	Titi monkey*	Tamarin*
Petomo	*Oenocarpus batava*	6	65	S			
Various	*Inga spp*	4	37	G	G	G	G
Nontoca	*Mauritia flexuosa*	5	29				
Dagenka	*Bactris gasipaes*	4	28				G
Tepenka	*Theobroma subincanum / Theobroma cacao*	4	21	G	G		
Opogenka	*Astrocaryum chambira*	3	13	S			
Yohuemo	*Pourouma cecropifolia*	4	11	G	G	G	S
Oboye	*Cleidion amazonicum*	3	3				
Daboka	*Solanum sessiliflorum*	1	1	G	G		
Minika	*Unknown*	1	1				
Mangomeg	*Cecropia sciadophylla*	0	1**	S	G	S	S

* Data available to species level.

** Observed consumed by S Papworth, not present in diaries

Table A2.3. Factors explaining cultural salience of 31 mammal species for the Waorani. Number of individuals in diet = IND.

Model	**AICc**	**ΔAICc**	**Model weight**
IND	-62.6	0.00	0.27
IND + Trade	-62.6	0.02	0.27
IND + Trade + IND x Trade	-61.0	1.57	0.13
IND + Trade + Primate	-60.6	1.96	0.10
IND +Primate	-60.3	2.25	0.09
IND + Trade + Primate + IND x Trade	-58.3	4.23	0.03
IND + Trade + Primate + Primate x Trade	-57.9	4.65	0.03
IND + Trade + Primate + Primate x IND	-57.8	4.78	0.03
IND + Primate + Primate x IND	-57.5	5.11	0.02
IND + Trade + Primate + IND x Trade +Primate x Trade	-57.3	5.30	0.02
IND + Trade + Primate + Primate x Trade +Primate x IND	-55.2	7.34	0.01
IND + Trade + Primate + IND x Trade +Primate x IND	-55.0	7.56	0.01
IND + Trade + Primate + IND x Trade +Primate x IND + Primate x Trade	-53.8	8.72	0.00
Trade	-34.6	28.01	0.00
Primate + Trade	-32.2	30.04	0.00
Primate + Trade + Primate x Trade	-30.5	32.04	0.00
Primate	-22.7	39.91	0.00
Null	-22.6	39.96	0.00

Variable importance	IND = 1.00; Trade = 0.62; Primate = 0.33; IND x Trade = 0.19, IND x Primate = 0.06, Trade x Primate = 0.06

APPENDIX 3

R code to reproduce analyses in Chapter 4.

```
#R code to model NSD, BRB and RUF. This file is best viewed in free downloadable
#software Tinn R, available from http://sourceforge.net/projects/tinn-r/

#Start with a tab delimited text file. Coordinates are measured in metres,
#and file has columns the with following data for each location,
#in chronological order within an individual and trip:
#Date - date on which location recorded dd/mm/yyyy
#Time - time at which location recorded hh:mm:ss
#IND: - unique reference code for each individual
#Latitude - Latitudinal reference in metres
#Longitude - Longitudinal reference in metres
#Trip - unique reference code for each trip

#load the required packages. This code will work with R 2.13.3
#and most recent versions (in December 2011) of the below packages.
#The code may not run perfectly if you are using older or newer versions
#To run this code, you have have to download additional packages
#Before you use a package for the first time you need to download it:
```

```
#Packages>Install Packages(s)
#select the CRAN mirror closest to you
#select the package from the list and click ok
#The exception to this is the package ruf
#before you use it the first time, remove the # from the following line
#install.packages("ruf",repos="http://www.csde.washington.edu/~handcock")
#then send to R to load the package
library(trip)
library(stringr)
library(adehabitatHR)
library(nlme)
library(lattice)
library(gmodels)
library(spatstat)
library(ruf)
library(maptools)

#example dataset can be downloaded from http://www.iccs.org.uk/sarahpapworth.htm
#Note: this is a computer generated data set, intended to demonstrate the use
#and outputs of this method. Data from the study is not available for public use,
#to protect the identities and activities of the participants.

#open the file in R
```

```
d1<-read.table("h:\\Papworth et al example data.txt",header=T)
##change date and time to the class POSIXct, so that the package adehabitat can
#create a trajectory of your locations

datetime <- as.POSIXct(paste(d1$Date,d1$Time),
format = "%d/%m/%Y %H:%M:%S",
"GMT") #reference time: If your locations are recorded in the file using local
#time, use "GMT". If they are global time, specify the hour band location, e.g.
# "America/Lima"


##make a data.frame of latitude and longitude. Here the raw values are divided
#by 1000 so that trajectories are calculated using km as the unit of measurement
coord<-data.frame((d1$Latitude),(d1$Longitude))
# make ltraj: a trajectory of all the relocations
d2<-as.ltraj(coord,datetime,
d1$INE,       #separate your data by individual.
burst=d1$Trip, #burst is used to creat subdivisions within an individual.
typeII=TRUE)      #typeII can be TRUE: radio-track data, or FALSE: not time
                 #recorded, such as tracks in the snow
summary(d2)
#you should now be able to see a summary of the trajectory data,
#with one line for each burst
```

```
#you can now make your trajectory regular, as radio tracks tend to lose
#a few seconds / minutes with each relocation
#firstly add "NA" for each missing location in your trajectory
d3<-setNA(d2,
as.POSIXct("2009-10-21 16:30:30"), #any time before earliest timedate in huntGPS
60,          #stating there should be a location every 60th time unit
tol=30,      #how many time units to search each side of expected location
units="sec")   #specifying the time units


#you can now make your trajectory regular
#firstly create a reference start time
refda <- strptime("00:00:30", "%H:%M:%S")   #all relocations should be altered
#to occur at 30 seconds past each minute
d4<-sett0(d3, refda,
60,                   #stating the interval at which relocations should be
correction.xy =c("none"),   #if "cs" performs location correction based on the
#assumption the individual moves at a constant speed
tol=30,      #how many time units to search either side of an expected location
units = "sec")  #specifying the time units


#to view your regular trajectory of points with NA's
summary(d4)
```

```
#now calculating NSD for each point
datansd<-NULL
for(n in 1:length(summary(d4)[,1])) #stating that NSD should be
#calculated separately for each burst
{
nsdall<-d4[[n]][,8]          #extracting the NSD for each location
nsdtimeall<-d4[[n]][,3]       #extracting the time for each location
nsdtimestartzero<-d4[[n]][,3]-d4[[n]][1,3]
#extracting the time since trip start for each location
nsdid<-rep(as.vector(summary(d4)[n,1]),
length.out=summary(d4)[n,3])
#extracting the individual associated with each location
nsdtrip<-rep(as.vector(summary(d4)[n,2]),length.out=summary(d4)[n,3])
#extracting the trip associated with each location
datansd1<-data.frame(nsdall,nsdtimeall,nsdtimestartzero,nsdid,nsdtrip)
#joining all these variables together in a data frame
datansd<-rbind(datansd,datansd1)
#joining all the data frames together
}
datansd$zero1<-as.numeric(unclass(datansd$nsdtimestartzero))
# making seconds since trip start numeric
datansd$zerostart<-datansd$zero1/60
#changing the time since trip start from seconds to minutes
```

```
datansd$minslitr2<-as.numeric(strftime(as.POSIXlt(datansd$nsdtimeall),
format="%M"))
#making a vector of the hour of the day a location occured
datansd$hdaylitr2<-as.numeric(strftime(as.POSIXlt(datansd$nsdtimeall),
format="%H"))
#making a vector of the minute in an hour a location occured
datansd$minsday<-((datansd$hdaylitr2*60)+datansd$minslitr2)
#calculating the minute in the day a location occured

summary(datansd)

#To select and name the hunting trips
hunt2<-c(5,6,8,10,11,12,14,15,19,22,24,26,27,28,30,31)
#a list of all numbers of all the hunting trips
datansd$hunt<-match(datansd$nsdtrip,hunt2,nomatch=0)
#assigning the value 0 to all non-hunting trips
datansd$hunt[datansd$hunt > 1] <- 1  #assigning the value 1 to all hunting trips
datansd$HUNT<-as.factor(datansd$hunt) #making it a factor
datansd1<-na.omit(datansd)          #remove NA's
datansd1$coordinates<-coord          #add the coordinates for each point
#you now have the dataframe you need (datansd1) to start analysis
#if the computer is slow, you can remove all the data sets you don't need
#to help it speed up
```

```
rm(d1)
rm(d2)
rm(d3)
rm(d4)
rm(coord)
rm(datetime)
rm(nsdid)
rm(nsdtimeall)
rm(nsdtimestartzero)
rm(nsdtrip)
rm(refda)


#NSD


#Now you can start modelling NSD using nlme. The book:
#Pinheiro and Bates (2004) Mixed-effects models in S and S-Plus.
#Springer Science: New York, can help, as will
#Bunnefeld at al (2011) A model-driven approach to quantify migration patterns:
#individual, regional and yearly differences.
#Journal of Animal Ecology 80: 466 - 476


#first model the data without random effects using nls, a least squares method
```

```
#this will help identify parameter estimates for use with nlme
m1<-nls(nsdall ~  asym /(1+exp((xmidA-zerostart)/scale1)) +
(-asym / (1 + exp((xmidB-zerostart)/scale2))), #this part defines eqn 1
start = c(asym=40000,xmidA=10,xmidB=30,scale1=4,scale2=4)
#these are the starting values for each parameter of the equation
,data=na.omit(datansd1))   #this is the data
summary(m1)       #this will print a summary of the converged model
#graphical exploration of the data will help you find sensible starting values
#for each of the parameters asym, xmidA, xmidB, scale1 and scale2.
#to graph nsd against time, use:
xyplot(nsdall~zerostart|nsdtrip,data=datansd1)
#Alternately, you can start with a single individual such as "SA" below, and
#gradually add one individual at a time.
m2<-nls(nsdall ~  asym /(1+exp((xmidA-zerostart)/scale1)) +
(-asym / (1 + exp((xmidB-zerostart)/scale2))),
start = c(asym=40000,xmidA=10,xmidB=30,scale1=4,scale2=4)
,data=na.omit(datansd1[datansd1$nsdid=="A",]))   #to specify only one individual
summary(m2)
#try various starting values - the model will only converge if the values are
#sufficiently close to the modelled values
#now try and model the data including random effects
#start with no variation in the explanatory variable
m3<-nlme(nsdall ~  asym /(1+exp((xmidA-zerostart)/scale1)) +
```

```
(-asym /(1 + exp((xmidB-zerostart)/scale2))), #the equation

fixed = list(asym+xmidA+xmidB+scale1+scale2~1),  #fixed effects

random= asym ~ 1|nsdid, #random effects: asym varies between individuals

start = c(asym=40000,xmidA=10,xmidB=30,scale1=4,scale2=4)

#starting vlaues for the parameters in the equation

,data=na.omit(datansd1))      #the data

print(AIC(m3))          #this will print the AIC of the converged model

#you can change the random effect structure

m4<-nlme(nsdall ~  asym /(1+exp((xmidA-zerostart)/scale1)) +

(-asym /(1 + exp((xmidB-zerostart)/scale2))),

fixed = list(asym+xmidA+xmidB+scale1+scale2~1),

random= asym ~ 1|nsdid/nsdtrip,       #random effects: asym varies between

#individuals, and also between trips within a single individual

start = c(asym=38000,xmidA=9,xmidB=30,scale1=3,scale2=3)

,data=na.omit(datansd1))

print(AIC(m4))


#When you have the best random effects structure, you can model the data with

#differences between your groups

m5<-nlme(nsdall ~  asym /(1+exp((xmidA-zerostart)/scale1)) +

(-asym / (1 + exp((xmidB-zerostart)/scale2))),

fixed = list(asym+xmidA+xmidB+scale1+scale2~HUNT), #just change this to say HUNT

random= asym ~ 1|nsdid/nsdtrip,
```

```
start = c(asym=40000,20000,xmidA=10,0,xmidB=30,0,scale1=3,0, scale2=3,0)

#and remember to add the extra parameters here: the first value for each

#parameter is the expected value for "0", and the second value is the

#difference between group "1" and group "0"

,data=na.omit(datansd1))

print(AIC(m5))

#now show a summary of the best model

summary(m5)

#you can show the fitted values

fitted(m5)

#normal probability plots

qqnorm(m5)

#the residuals

plot(m5)

#and estimate the 95% confidence intervals for the parameter estimates

#first make a matrix of all the posible constrasts: the matrix below is

#applicable if you are comparing two groups

matrix.contrasts<- rbind(c(1,0,0,0,0,0,0,0,0,0),

                 c(1,1,0,0,0,0,0,0,0,0),

                 c(0,0,1,0,0,0,0,0,0,0),

                 c(0,0,1,1,0,0,0,0,0,0),

                 c(0,0,0,0,1,0,0,0,0,0),

                 c(0,0,0,0,1,1,0,0,0,0),
```

```
                    c(0,0,0,0,0,0,1,0,0,0),
                    c(0,0,0,0,0,0,1,1,0,0),
                    c(0,0,0,0,0,0,0,0,1,0),
                    c(0,0,0,0,0,0,0,0,1,1))
#estimate the 95% confidence intervals
estint<-estimable(m5, matrix.contrasts, conf.int=0.95) #you can change this
#to estimate different confidence intervals
#To define the peak of the curve, derive estimated NSD values for the 1st group
peakHUNT1<-estint[1,1]/ (1+exp((estint[3,1]-(0:400))/estint[7,1])) +
(-estint[1,1])/(1+exp((estint[5,1]-(0:400))/estint[9,1]))
#find the maximum predicted value, representing the peak of the curve
PH1<-max(peakHUNT1)
#squareroot this to demonstrate the actual distance travelled
sqrt(PH1)
#repeat for the second group
peakHUNT2<-estint[2,1]/ (1+exp((estint[4,1]-(0:400))/estint[8,1])) +
(-estint[2,1])/(1+exp((estint[6,1]-(0:400))/estint[10,1]))
#find the maximum predicted NSD value, representing the peak of the curve
PH2<-max(peakHUNT2)
#squareroot this to demonstrate the actual distance travelled
sqrt(PH2)
#you can also make a graph like figure 3
#create a window that is divided in two (one for hunting and one for
```

```
#non-hunting trips


par(mfrow=c(2,1))
#plot the best model
#this uses the parameters from the model to predict the curve for NSD
datansd1$pred<-predict(m5,level=0) #remember to put in the correct model here
myPanel <- function(x,y, ...){
panel.xyplot(x,y, ...)
dotArgs <- list(...)
# select the appropriate rows of data and predict and then order them
predY <- datansd1$pred[dotArgs$subscripts]
predX <- datansd1$zerostart[dotArgs$subscripts]
ord <- order(predX)
predX <-  predX[ord]
predY <-  predY[ord]
# add as a panel line
panel.lines(predX, predY, col='black', type='l',lwd=2)
}
#now plot the data with the predicted curve
xyplot(nsdall ~ zerostart|HUNT, data=datansd1,
col="grey",    #color for the observed locations
type='b',      # 'b' shows the locations as dots, with a line connecting
```

```
#successive locations. Can also be 'p' for just the locations, or 'l' for just
#the line between locations
ylab=expression(paste('Net squared displacement ',' ', (km^2))), #y axis label
xlab="Minutes after trip start",                              #x axis label
group=nsdtrip,           #grouping factor  - changed from nsdTRIP: important??
panel=myPanel,           #predicted values from above
strip=strip.custom(bg="grey", factor.levels=c('Non-hunting trips (n=17)',
'Hunting trips (n=19)'  )),  #to create a strip at the top to label each group
scales=list(x=list(alternating=1,
at = c(0,10,20,30,40,50,60)),tck=-1,       #locations of marks on the x axis
y=list(alternating=1,
at=c(0,20000,40000,60000,80000,100000,120000,140000,160000),tck=-1) #locations
#of marks on the y axis
))


#to select the relevant data identified using NSD
#Group 1: non hunting trips
nothunt<-datansd1[datansd1$HUNT=="0",] #select the non hunting data
nothunt1<-na.omit(nothunt)   #remove the NA's generated by removing hunting data
nothunt1$include[nothunt1$zerostart > 18] <- 1    #select all locations where
#time after trip start is greater than 60
nothunt2<-na.omit(nothunt1)                    #remove the NA's generated
nothunt2$include1[nothunt2$zerostart < 24] <- 1  #select all the locations
```

```
#where time after time start is smaller than 265
nothunt3<-na.omit(nothunt2)                    #remove the NA's generated
#Group 2: hunting trips
huntdata<-datansd1[datansd1$HUNT=="1",]            #select the hunting data
huntdata1<-na.omit(huntdata)                   #remove the NA's generated by
#removing non hunting data
huntdata1$include[huntdata1$zerostart < 24] <- 1 #select all the locations
#where time after trip start is smaller than 273
huntdata2<-na.omit(huntdata1)                  #remove NA's generated
#nothunt3 and huntdata2 have an unequal number of column
#(nothunt3 has an additional column named "include1")
#in order to join the two, we need to add an additional column to huntdata2
huntdata2$include1<-huntdata2$include
#join the two data sets together
d5<-rbind(huntdata2,nothunt3)


#BRB
#useful reading includes:
#Benhamou (2011) Dynamic Approach to Space and Habitat Use Based on Biased
#Random Bridges. PLoS ONE 6: e14592
#Benhamou and Cornelis (2010) Incorporating movement behaviour and barriers to
#improve kernel home range space use estimates. Journal of Wildlife Management
```

```
#74: 1353 - 1360
#Calenge (2011) Home range estimation in R: the adehabitatHR package.
#from: cran.r-project.org/web/packages/adehabitatHR/vignettes/adehabitatHR.pdf
#now check to see how many locations you have for each individual
summary(d5$nsdid)
#remove individuals from the data set which have too few locations to estimate
#UD using BRB
notenough<-c("B")   #the names
#of individuals with insufficient data
d5$insufficient<-match(d5$nsdid,notenough,nomatch=0)      #label all
#the individuals with sufficient data with a 0
d5$insufficient[d5$insufficient > 1] <- 1   #label all the individuals
#with insufficient data with a "1"
d5$INSUF<-as.factor(d5$insufficient)      #make insufficient a factor
d6<-d5[d5$INSUF=="0",] #select individuals with sufficient data
d7<-na.omit(d6)           #remove the NA's
d7<-d5
#to show a summary of the points for each trip, for each individual, use
table(d7$nsdtrip,d7$nsdid)
#create a new trajectory with refined data set, divided by individual and trip
d8<-as.ltraj(d7$coordinates,d7$nsdtimeall,d7$nsdid,
burst=d7$nsdid,typeII=TRUE)
summary(d8)
```

```
#make a 10m x 10m grid square of study area
xpoints<-c(346540:346670)#specific the extent of the study area on a global grid
xpoints1<-xpoints*10    #in metres, removing the last 2 digits
ypoints<-c(926080:926190)   #do the same for the y axis
ypoints1<-ypoints*10
pts = expand.grid(x = xpoints1, y = ypoints1)   #make the grid
grd.pts = SpatialPixels(SpatialPoints(pts)) #it has to be SpatialPixels to use
#in BRB
#calculate the diffusion parameter D for the BRB. BRB.lik is also available to
#estimate D
diffusion<-BRB.D(d8, #the new trajectory
Tmax = 5*60,            #the maximum time between relocations where
#smoothing should occur. Measured in seconds, so 120*60 for 120 mins, or 2 hours
Lmin = 0)               #The smallest distance at which an animal should be
#considered moving, and therefore modelled in the UD. 0 if all data is included.
#make a UD using BRB
#first get a good value for hmin - use:
summary(d8[[1]])
#to find the mean distance travelled between locations
d9<-BRB(d8, #the trajectory
diffusion,          #the diffusion parameter
Tmax=5*60,  #maximum time between relocations: should be the same as smootherD
Lmin=0,     #the same as for "diffusion"
```

```
hmin=35,      #minimum smoothing parameter in units of locations
#should be > mean interlocation distance/2
grid = grd.pts,  #the gird in which to estimate UD
b = FALSE,       # If TRUE, the relocation variance progressively merges with
#the movement component; if FALSE, the relocation variance has a constant weight
same4all = FALSE, #has to be FALSE if a grid is specified. If no grid is
#specified, can be TRUE so the UD is estimated in the same area for each
#individual
extent=0.1,  #extent of the grid used for estimation
tau=20)      #frequency of modelled relocations between known points.
#Measured in seconds
kerneloverlaphr(d9,    #to calculate overlap between trips
method = c("HR"),      #type of overlap. HR is the proportion of the home range
                      #of one individual / trip used by another
percent = 95)          #Use percentage of home range for calculating overlap
#Extract the UD for each individual
d9a<-getvolumeUD(d9[[1]])   #select the UD for the first individual
#calculating the  are of use
IND1Area<-kernel.area(d9a,percent=seq(50,95,by=5))   #to get the area
#(in hectares) inside each % use between 50 and 95, at 5% intervals
IND1Area        #show the areas calculated
d9a1<-as.data.frame(d9a)   #change into a data frame that can be used by ruf
summary(d9a1)                  #check it looks ok
```

```
d9a1x<-data.frame(d9a1$Var1,d9a1$Var2,d9a1$n) #change dataframe variable
#order, as X and Y need to be the first two columns to use as.ppp
names(d9a1x)<-c("X","Y","UD")  #change the names to more sensible ones
d9a1x$include1[d9a1x$UD < 99] <- 1
#d9a1x$include1[d9a1x$UD < 99] <- 1  #assign 1 to any grid square where UD < 99
IND1<-na.omit(d9a1x)          #remove the grid squares where UD > 99
#open table and move X and Y to be the first columns
coord<-data.frame(IND1$X,IND1$Y)  #create new data frame with all grid
#coordinates
xysp<-SpatialPoints(coord)      #make the data frame into class "SpatialPoints",
#so it can be used to make a Minimum Convex Polygon
cp<-mcp(xysp,percent=100)      #create the minimum convex polygon
MCP<-as(cp, "owin")     #turn it into class "owin", so it can be used with the
#function "nncross"
Resource<-as.ppp(IND1,MCP)  #create an object of class ppp which specifies
#research area to use with nncross
Community<-c(9261222,3466080)    #location of the community
C1<-as.ppp(Community,MCP)    #make this class ppp so it can be used with nncross
Community1<-nncross(Resource,C1)#calculate distance between locations and the
#community
IND1$community<-Community1[,1]   #add the measurements to the datafile
#alternately you can load shapefiles
R<-readShapeSpatial ("h:\\River1.shp")   #1. load your shapefile
```

```
R1<-as.psp(R)    #2. make an object of class psp with your shapefile
River<-nncross(Resource,R1)  #3. for each point in the ppp "Resource",
#calculate the distance to the nearest point in "River"
IND1$river<-River[,1]      #4. add these distances to your datafile with UD
#repeat 1-4 for each landscape feature
#drawing the heatmap of UD shown in Figure 3
image(d9a,         #specify the data to use
col=heat.colors       #specify color scheme
(50))                #specify how many different colors to use

xyzv<-as.image.SpatialGridDataFrame(d9a)    #create an object with the
#information required to add contours of use
contour(xyzv,        #contour information
levels=c(50),        #which % use contour to add
drawlabels=FALSE,     #can be TRUE or FALSE. If TRUE, adds a label of the % use
# of the contour. If FALSE, no label added
lwd=2,               #width of the added contour line
add=TRUE)            #can be TRUE or FALSE. If TRUE, contour line will be
#added to the existing image. If FALSE, a new image will be drawn
contour(xyzv,levels=c(95),           #to add 95% contour
drawlabels=FALSE,lwd=2,lty=2,add=TRUE)  #with a dashed line (lty=2)
plot(R,col="black",pch=19,cex=40,add=TRUE) #if you wish to add landscape
#features
```

```
#RUF

#Read: Marzluff et al (2004) Relating resources to a probabilistic measure of
#space use: Forest fragments and Streller's Jays. Ecology 85: 1441 - 1427
#before starting


#check if your variables need to be transformed
#if UD distribution is heavily biased to higher percentages, consider 100-UD
hist(IND1$UD)              #to view a histogram of UD
IND1$UD2<-100-IND1$UD    #create a new variable where distribution will be
#biased to lower numbers, and therefore can be normalised using the natural log
#if explanatory variables cannot be normalised, or have another unusual
#distributions (i.e. strongly binomial), change them to categorial variables
#now fit each possible model and calculate the AIC
model1 <- ruf.fit(log(UD2)     #you can log, sqrt, asin your response variable
~sqrt(community)+sqrt(river),  #put your explanatory variables here
space= ~ X + Y,              #specify which dataframe variables represent
#latitude and longitude
data=IND1,                #which dataset to use
theta=c(0.2,2),              #which values to use for the Malvern correlation
#function. The first number is the range, which is the starting point from which
```

```
#ruf.fit will choose the best value for the range. It's a good idea to start
#with a low number. It is measured in metres. The second value is a smoothness
#parameter. It can be 0+, up to 10. It will not be estimated by ruf.fit - you
#need to vary it and choose the value which lowers to Malvern logLikelihood
standardized=FALSE)        #can be TRUE or FALSE. If FALSE, estimates for
#different indivuals can be compared to calculate a population estimate.
#If TRUE, all the estimates for all variables are shown on the same scale
#(within a single model), and the relative importance of each variable
#can be estimated.
summary(model1)        #to show results
```

APPENDIX 4

Characteristics of red titi monkey focal group calls and models used for analysis

Table A4.1: Summary table of characteristics of all morning choruses given by focal groups. As good quality recordings of the morning choruses of focal groups were available, active calling time was measured to the nearest second for each calling bout. Calling bouts were separated by 60 seconds of silence.

Site	Group (maximum observed group size during study)	Number of observation mornings calling, n=7 (%)	Season (IHP = increased hunting pressure, DHP = decreased hunting pressure)	Start time of first bout	Start time relative to sunrise	End time of last bout	Active calling time (seconds)	Number of calling bouts
High hunting pressure	Ceiba (4)	2 (29%)	IHP	06:42	37	07:19	113	1
			DHP	07:06	66	07:07	156	1
	Estacion (6)	2 (29%)	DHP	05:38	-10	05:41	149	1
				05:45	-15	07:13	244	5
	Laguna (3)	0 (0%)	NA	NA	NA	NA	NA	NA
	Mirador (2)	3 (43%)	IHP	05:59	-2	06:01	74	1
			DHP	05:44	-3	06:00	95	2
				07:21	79	08:29	360	1
	Napo (4)	1 (14%)	DHP	07:13	64	07:39	266	9
	Parcela (4)	1 (14%)	DHP	06:01	11	06:01	NA*	NA*
Low hunting pressure	Chichico (2)	5 (71%)	IHP	05:57	-9	06:00	174	1
				06:02	-6	06:02	NA*	NA*
				05:40	-28	05:43	176	1
			DHP	06:55	65	07:07	262	1
				07:15	90	07:22	121	1
	Chorongo (3)	0 (0%)	NA	NA	NA	NA	NA	NA
	Guacamayo (5)	4 (57%)	IHP	05:54	-14	05:59	207	1
				07:58	111	07:58	66	1
			DHP	06:41	34	06:42	74	1
				05:30	-15	07:12	393	2
	Harpia (2)	4 (57%)	DHP	05:53	-16	05:56	108	1
				06:52	44	07:05	189	3
			IHP	05:32	-42	08:38	165	3
				05:51	-1	06:41	NA*	NA*
	Matamata (6)	2 (29%)	DHP	06:56	53	07:01	233	2
				07:22	68	07:28	204	1
	Puma (2)	2 (29%)	IHP	06:10	25	08:04	389	2
			DHP	07:07	82	07:13	242	2

---

* Recording not available due to battery failure of Marantz digital recorder

Table A4.2. Mixed effect models for two measures of sound propagation; SNR and median amplitude (n=30). Random effect variables playback location nested in site were included in all models. The differences in AICc (Aikaike's information criterion adjusted for small sample sizes) between each model and the best model.

Measure	**Null model**	**Distance**	**Interaction between distance and site**
SNR	17.33	0	3.81
Median amplitude	49.74	0	4.47

Table A4.3. Binomial fixed effects of models with whether focal groups were heard as a dependant variable (n=84). Random effect variables for focal group nested within site were included in all models. The table indicates the fixed-effect variables included in each model, the AICc (Aikaike's information criterion adjusted for small sample sizes), the difference between AICc for the presented model and the best fitting model (ΔAICc), and the model weights.

Model	**AICc**	**ΔAICc**	**Weight**
Site+Cloud cover	104.46	0.00	0.20
Site	104.48	0.03	0.20
Cloud cover	105.74	1.28	0.10
Null	105.99	1.54	0.09
Season+Site	106.56	2.10	0.07
No. Previous callers+Site	106.59	2.13	0.07
No. Previous callers+Site+Cloud cover	106.63	2.18	0.07
Season+Site+Cloud cover	106.65	2.19	0.07
Season+Cloud cover	107.85	3.39	0.04
No. Previous callers+ Cloud cover	107.87	3.41	0.04
Season	107.96	3.51	0.03
No. Previous callers	108.05	3.60	0.03

Variable weights (W_i): Site = 0.66, Cloud cover = 0.51, Season = 0.21, No. Previous callers = 0.20, Season:Site = 0.05

Table A4.4. Negative binomial fixed effects of models with number of audible groups on an observation morning as a dependant variable (n=84). Random effect variables for focal group nested within site were included in all models. The table indicates the fixed-effect variables included in each model, the AICc (Aikaike's information criterion adjusted for small sample sizes), the difference between AICc for the presented model and the best fitting model (ΔAICc), and the model weights.

Model	**AICc**	**ΔAICc**	**Weight**
Season	314.13	0.00	0.52
Season+Cloud cover	315.93	1.80	0.21
Season+Site	316.07	1.94	0.20
Season+Site+Cloud cover	317.90	3.77	0.08

Variable weights (W_i): Season = 1.00, Site = 0.27,cloud cover = 0.29

Table A4.5. Gaussian fixed effects of models with difference of start time of first call by each group to sunrise on the observation day as a dependant variable (n=162). Random effect variables for observation day and observation location nested within site were included in all models. The table indicates the fixed-effect variables included in each model, the AICc (Aikaike's information criterion adjusted for small sample sizes), the difference between AICc for the presented model and the best fitting model (ΔAICc), and the model weights.

Model	**AICc**	**ΔAICc**	**Weight**
Season+Site+Season:Site	1696.32	0.00	0.35
Season+Site	1697.58	1.26	0.18
Season+Site+Cloud cover+Season:Site	1698.29	1.97	0.13
moon+Season+Site+Season:Site	1698.46	2.14	0.12
Season	1699.10	2.78	0.09
moon+Season+Site	1699.41	3.09	0.07
Season+Site+Cloud cover	1699.70	3.38	0.06

Variable weights (W_i): Season = 1.00, Site = 0.91, Season: Site = 0.59, lunar phase = 0.19, Cloud cover = 0.19

Table A4.6. Negative binomial distribution fixed effects of models with end time of last call as a dependant variable. Random effect variables for observation day and observation location nested within site were included in all models (n=162). The table indicates the fixed-effect variables included in each model, the AICc (Aikaike's information criterion adjusted for small sample sizes), the difference between AICc for the presented model and the best fitting model (ΔAICc), and the model weights.

Model	**AICc**	**ΔAICc**	**Weight**
Season+Site+Season:Site	1720.64	0.00	0.48
Season+Site+Cloud cover+Season:Site	1721.89	1.25	0.26
Season	1723.17	2.53	0.14
Season+Site	1723.36	2.72	0.12

Variable weights (W_i): Season = 1.00, Site = 0.86, Season:Site = 0.74, Cloud cover = 0.26

Table A4.7. Negative binomial fixed effects of models with time actively calling by each audible group on an observation day as a dependant variable (n = 162). Random effect variables for observation day and observation location nested within site were included in all models. The table indicates the fixed-effect variables included in each model, the AICc (Aikaike's information criterion adjusted for small sample sizes), the difference between AICc for the presented model and the best fitting model (ΔAICc), and the model weights (W_i).

Model	**AICc**	**ΔAICc**	**Weight**
Season+Site+Season:Site	892.24	0.00	0.22
Null	893.40	1.15	0.13
Season+Site+Season:Site+Cloud cover	893.54	1.30	0.12
Site	893.98	1.73	0.09
total no groups+Season+Site+Season:Site	894.17	1.92	0.09
Total in day	894.45	2.21	0.07
Season+Site+Cloud cover+Total in Day+ Season:Site	894.86	2.62	0.06
Season	895.08	2.83	0.05
Season+Site	895.44	3.20	0.05
Cloud cover	895.47	3.23	0.04
Site+Total in day	895.65	3.41	0.04
Site+Cloud cover	896.05	3.80	0.03

Variable weights (W_i): Season=0.70, Site=0.59, Season:Site=0.49, Cloud cover=0.26, Total in day=0.26

APPENDIX 5

Characteristics of red titi monkey focal group calls and models used for analysis

Table A5.1: Summary table of characteristics of all morning choruses given by focal groups. As good quality recordings of the morning choruses of focal groups were available, active calling time was measured to the nearest second for each calling bout. Calling bouts were separated by 60 seconds of silence.

Site	Group (maximum observed group size during study)	Number of observation mornings calling, n=7 (%)	Season (IHP = increased hunting pressure, DHP = decreased hunting pressure)	Start time of first bout	Start time relative to sunrise	End time of last bout	Active calling time (seconds)	Number of calling bouts
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Table A5.2. Mixed effect models for two measures of sound propagation; SNR and median amplitude (n=30). Random effect variables playback location nested in site were included in all models. The differences in AICc (Aikaike's information criterion adjusted for small sample sizes) between each model and the best model.

Measure	**Null model**	**Distance**	**Interaction between distance and site**
SNR	17.33	0	3.81
Median amplitude	49.74	0	4.47

Table A5.3. Binomial fixed effects of models with whether focal groups were heard as a dependant variable (n=84). Random effect variables for focal group nested within site were included in all models. The table indicates the fixed-effect variables included in each model, the AICc (Aikaike's information criterion adjusted for small sample sizes), the difference between AICc for the presented model and the best fitting model (ΔAICc), and the model weights.

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Season	107.96	3.51	0.03
No. Previous callers	108.05	3.60	0.03

Variable weights (W_i): Site = 0.66, Cloud cover = 0.51, Season = 0.21, No. Previous callers = 0.20, Season:Site = 0.05

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Table A5.5. Gaussian fixed effects of models with difference of start time of first call by each group to sunrise on the observation day as a dependant variable (n=162). Random effect variables for observation day and observation location nested within site were included in all models. The table indicates the fixed-effect variables included in each model, the AICc (Aikaike's information criterion adjusted for small sample sizes), the difference between AICc for the presented model and the best fitting model (ΔAICc), and the model weights.

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Model	**AICc**	**ΔAICc**	**Weight**
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Season+Site+Cloud cover+Season:Site	1721.89	1.25	0.26
Season	1723.17	2.53	0.14
Season+Site	1723.36	2.72	0.12

Variable weights (W_i): Season = 1.00, Site = 0.86, Season:Site = 0.74, Cloud cover = 0.26

Table A5.7. Negative binomial fixed effects of models with time actively calling by each audible group on an observation day as a dependant variable (n = 162). Random effect variables for observation day and observation location nested within site were included in all models. The table indicates the fixed-effect variables included in each model, the AICc (Aikaike's information criterion adjusted for small sample sizes), the difference between AICc for the presented model and the best fitting model (ΔAICc), and the model weights (W_i).

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Variable weights (W_i): Season=0.70, Site=0.59, Season:Site=0.49, Cloud cover=0.26, Total in day=0.26