Human-macaque encounters in Ifrane National Park, Morocco: behavioural, spatial, and temporal coping strategies of the Barbary macaque (*Macaca sylvanus*)

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Abstract

Wild animals in human-dominated landscapes are exposed to a broad range of human activities and infrastructure that have the potential to alter their fitness and behaviour. Understanding wildlife responses to human disturbance is an important conservation goal, particularly when the fate of many wildlife populations depends on their capacity to coexist with humans. Most field studies have focussed on the effects of one type of disturbance only (i.e. a single disturbance type per study), however in heavily human-modified habitats animals must often deal with numerous different types of human activity and infrastructure, and less is known about whether different types differentially affect animal behavioural responses.

This study examined the responses of 5 wild Barbary macaque (*Macaca sylvanus*) groups in Ifrane National Park, Morocco, to a range of human activities and infrastructure on a short-term behavioural scale (individual focal follows) and a longer-term spatio-temporal scale (individual scan sampling). Using a series of GLMMs I first compared pre-, during-, and post- human-macaque encounter levels of escape, affiliative, and self-directed behaviours (behaviours that may serve as components of a coping strategy) to determine whether different encounter types differentially affect macaque behavioural responses. Using logistic regression to estimate resource selection functions I then examined the behaviour-specific habitat use of macaques to determine whether (and how) different types of human activity and infrastructure influence habitat selection within home ranges.

Two broadly consistent responses to human encounters were observed; the first in association with potentially threatening encounters (those that involved/potentially involved dogs), and the second with potentially rewarding encounters (those that involved human provisioning). In response to potentially threatening encounters macaques made extensive use of escape behaviours, varied use of affiliative behaviours, and limited use of self-directed behaviours. In response to potentially rewarding encounters, macaques made use of escape, affiliative, and self-directed behaviours.

Three broadly consistent patterns of habitat selection/avoidance were observed in response to human activities and infrastructure within macaque home ranges. Macaques exhibited a general spatial preference for areas close to roads and a general spatial avoidance of both open areas (i.e. with no tree cover) and areas close to herding routes. Macaques also selected/avoided potentially threatening and rewarding areas (i.e. shepherd herding routes and provisioning loci) on a flexible temporal scale, only using potentially threatening areas when the probability of a human encounter was low, and preferentially using rewarding areas only when the risk/benefit balance associated with human provisioning was most heavily in their favour.

The results of this study highlight the value of considering the effects of multiple different types of human activity and infrastructure (at different spatio-temporal scales) on wildlife behaviour and welfare, and of assessing human impact on habitat selection separately for different types of behaviour. Such detailed studies on the effects of human activities on wild animal populations can enhance our understanding of, and ability to manage, the impacts of increasing human expansion into wildlife habitat.

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Chapter 1: General Introduction

Wild animals in human-dominated landscapes are exposed to a broad range of human activities and infrastructure that have the potential to alter their fitness and behaviour. Understanding wildlife responses to human disturbance is an important conservation goal, particularly when the fate of many wildlife populations depends on their capacity to coexist with humans. However, understanding the impact of human expansion on animal populations can be complicated by the fact that not all human-wildlife encounters have entirely negative outcomes. Many species are capable of successfully exploiting human activity and infrastructure. For example, parous moose (*Alces alces*) in Grand Teton National Park pre-emptively shield their neonates from road-averse brown bears (*Ursos arctos*) by shifting birth sites towards paved roads (Berger, 2007), and common ravens (*Corvus corax*) on the Arctic Coastal Plain of Alaska use elements of oil and gas exploration infrastructure as (non-natural) nest sites (Day, 1998). Most notable however is the way in which certain species exploit anthropogenic food sources.

Many wildlife species within human-modified habitats are attracted to and can benefit from increased access to human food, often in the form of refuse, crop-raiding, or active provisioning. Animal consumption of calorie-dense human food has been linked to increases in fertility rate (*Sus scrofa* - Cahill, Llimona, Cabañeros, and Calomardo, 2012), group size (*Canis latrans* - Lindsey, 1987), and population density (*Mungos mungo* - Gilchrist and Otali, 2002). It may also alter activity budgets by reducing foraging time and freeing individuals to, for example, rest more (e.g. *Papio cynocephalus* - Altmann and Muruthi, 1988; e.g. *Taurotragus derbianus* - Hejcmanová, Vymyslická, Zácková, and Hejcman, 2013; e.g. *Macaca sylvanus* - Unwin and Smith, 2010).

There are however considerable costs associated with human-modified habitats, human encounters, and human provisioning (both direct and indirect). The inclusion of human food into the diet of wild animals can contribute to the transmission of pathogens (Wilson, 1994) and to the development of obesity, diabetes, and nutritional deficiencies (Bauer, Arndt, Leslie, Pearl, and Turner, 2011; O'Leary and Fa, 1993; Semeniuk, Speers-Roesch, and Rothley, 2007). Provisioned animals also often experience a greater risk of injury and/or death when interacting closely with humans, both as a result of direct physical aggression (Zhao and Deng, 1992) and more frequently as a result of their proximity to human infrastructure, particularly roads (Samuels and Bejder, 2004;

Shackley, 1996). Roads that pass through wildlife habitat may become focal points for provisioning, increasing the risk of injury by vehicles. Grizzly bears (*Ursos arctos horribilis*) and northern cassowaries (*Casuarius unappendiculatus)* experience high mortality in association with roads and roadside feeding (Benn and Herrero, 2002; Crome and Moore, 1990), as do Japanese macaques (*Macaca fuscata*) fed from cars at Hakone, Japan (Okano, 2002).

Even in the absence of provisioning, animals that co-exist with humans experience a range of potential risks. Frequent human-wildlife encounters may habituate animals to the presence of humans in general, rendering them more vulnerable to those who wish them harm, e.g. poachers or hunters (Kasereka, Muhigwa, Shalukoma, and Kahekwa, 2006; Ménard et al., 2014a). They may also be more frequently exposed to other animals associated with human activity, particularly dogs (*Canis lupus familiaris*). Whether they are feral or in the care of humans (e.g. sheep or guard dogs), dogs represent a significant threat to wildlife (Young, Olson, Reading, Amgalanbaatar, and Berger, 2011), through disease transmission (Mamaev et al., 1995), intraguild competition (Vanak and Gompper, 2009), and predation (Bouvier et al., 1995; Lenth, Knight, and Brennan, 2008; Manor and Saltz, 2004).

It is clear therefore that a wide variety of human activities can alter wildlife behaviour. However most field studies have focussed on the effects of one type only (e.g. resource conflict (e.g. *Elephas maximus indicus* – Choudhury, 2004); deforestation (e.g. *Trachypithecus vetulus* and *Macaca sinica* - Nijman and Nekaris, 2010); (wildlife-tourism, (e.g. *Alouatta palliata Mexicana* - Aguilar-Melo et al., 2013; *Macaca sylvanus* - Maréchal, 2015); or human recreation (e.g. *Lepus timidus* - Rhenus, Wehrle, and Palme, 2014). Few studies have simultaneously examined the behavioural response of wildlife to multiple different types of human activity and infrastructure, and then, only at a single temporal scale (Lyon, 2012). In heavily human-modified habitats however, animals must often deal with numerous different types of human activity, infrastructure, and encounter, and less is known about whether different disturbance types differentially affect animal behavioural responses (Li, Monclús, Maul, Jiang, and Blumstein, 2011). The aim of this study is to contribute to that understanding by examining first the short-term behavioural responses of Barbary macaques (*Macaca sylvanus*) to various types of human encounter, and second their longer-term habitat-use responses to various types of human activity and infrastructure within their home ranges.

The Barbary macaque is an ideal species in which to examine the effects of human encroachment on wildlife habitat for several reasons. Firstly because they are members of the most taxonomically diverse and widespread primate genus (that as such comes into frequent contact with humans) (Fa, 1989; Thierry, 2011); secondly because they demonstrate an ability to adapt behaviourally to anthropogenic habitats (Fa, 1986b; Thierry, 2011); and thirdly because the most significant threats they face in the wild (habitat degradation and destruction, and the illegal live trade in infant macaques) are largely driven by the expansion of human populations and resource requirements (Ménard et al., 2014a). Barbary macaque habitat is under growing pressure from expanding human populations, activity, and infrastructure, and macaque numbers are (and have long been) in steady decline (Ciani et al., 2005; Taub, 1977; Van Lavieren and Wich, 2009). Once widespread throughout Europe and North Africa, the Barbary macaques' current distribution in the wild is limited to the introduced population on the Rock of Gibraltar and two highly fragmented wild populations in Morocco and Algeria. These are separated by a distance of approximately 700 km and the subpopulations therein persist in disjunct, relict forest patches with no corridors to link them (Fooden, 2007; Ménard et al., 2014b).

Barbary macaques live in large multi-male, multi-female groups (Thierry, Singh, and Kaumanns, 2004) of up to 80 individuals (in the wild) with a modal group size of 40 and an average of 27.1 (Ménard, 2002). Females reach sexual maturity at around 4-5 years old and are philopatric, i.e. they remain in their natal group for life. Males generally disperse, emigrating to another group when they reach sexual maturity at around 5-6 years of age, reducing the possibility of inbreeding and increasing the chance of finding viable mates (Kuester, Paul, and Arnemann, 1994; Ménard, 1996). Both male and female dominance hierarchies exist, however according to their patterns of aggression and reconciliation the species is classed as mildly 'tolerant' (grade 3 on a scale ranging from 1 (despotic/least tolerant) to 4 (egalitarian/most tolerant)) (Thierry, 2000). Conflicts are often resolved through the use of affiliative behaviours, dominance/submissive gestures, facial displays, and infant 'buffers' (Hesler and Fischer, 2007; Paul, Kuester, and Arnemann, 1996; Preuschoft, Paul, and Kuester, 1998).

The species is diurnal, arboreal, and terrestrial (reported mean frequency of daytime terrestriality varies from 68% to 83% in Morocco, and from 58% to nearly 100% in Algeria (Fooden, 2007)). They primarily forage on the ground for grass, roots, herbs, fruit, fungi, and invertebrates; and in the trees for leaves, sap, seeds, and occasionally bird chicks and eggs (Ménard, 2002; Young, Schülke, Ostner, and Majolo, 2012). The macaque population in Morocco experiences strong seasonal variations in climate, and thus resource availability (Hanya et al., 2011), requiring that the Barbary macaque be an eclectic forager and dietary generalist (Ménard, 2002).

The largest remaining wild Barbary macaque population is in the Middle Atlas Mountains of Morocco and is believed to contain approximately 5000 individuals (Ménard et al., 2014b). This represents a population decline of more than 50% over the last 3 generations (24 years) and in 2008 the species was classified as ‘Endangered’ by the International Union for Conservation of Nature (IUCN) (Butynski et al., 2008). The Barbary macaque’s decline over the last 20 years has been largely attributed to habitat loss (through the logging and degradation of cedar forests), overexploitation of forests (overgrazing by sheep and goats, and cedar pruning during livestock food shortages) (Ciani et al., 2005; Ménard et al., 2014a), and the removal of young macaques for the illegal pet trade (Ménard et al., 2014a; Van Lavieren, 2012).

These problems are characteristic of the situation within Ifrane National Park (INP). The park is situated in the Middle Atlas Mountains of Morocco and overlaps the range of the largest remnant population of wild Barbary macaques (Ménard et al., 2014b). A continual process of logging, pruning, clear-cutting, and overgrazing has resulted in the fragmentation of the forest into isolated, degraded patches. As a consequence, many Barbary macaque populations within INP, the Middle Atlas, and Morocco generally, are confined to highly fragmented, heavily human-modified habitats that overlap areas of human land use (Lamb, Damblon, and Maxted, 1991; Ménard et al., 2014b). As such they are unable to a) migrate away from the effects of human activity and infrastructure, b) obtain resources elsewhere, and/or c) colonise new areas; all of which may have previously been possible, prior to the fragmentation of the forest. This situation is exacerbated by the species’ social organisation (Ménard et al., 2014a). Only male Barbary macaques emigrate and they are incapable of colonising or recolonising new areas alone. Only through group fission can females disperse, however when new groups formed this way in Algeria they remained in the same forest patch as the parent group (Ménard and Vallet, 1993). It is unclear whether this was due to strong home range fidelity or to an unwillingness to cross open ground (several studies have confirmed that macaques seem unwilling to cross open areas (or abandon the forest edge) in excess of approximately 200 m (Taub, 1977; Ménard, 1996)), but the consequences are effectively the same. As such the macaques that remain in these forest fragments must find ways to cope with, and adapt to, encroaching human activity and infrastructure within their home ranges.

In keeping with the risk-disturbance hypothesis (Frid and Dill, 2002) many studies posit that an animal’s response to human disturbance should follow the same economic principles as those used by animals encountering predators (Gill and Sutherland, 2000). That is, because responses to predation risk and disturbance stimuli both divert time and energy away from fitness-enhancing activities, animals should attempt to minimise their costs in a similar way; by tracking and responding appropriately to short-term changes in risk/reward conditions (Frid and Dill, 2002; Gill and Sutherland, 2000; Lima and Dill, 1990). This provides a useful theoretical framework for making predictions and for understanding why particular responses occur, one which can be utilised by multiple studies across multiple species. For example, flight probability and initiation distance are predicted to increase when disturbance stimuli approach more directly, more quickly, are larger in size, larger in number, and when the distance from refuge is greater and flight costs lower (Frid and Dill, 2002). Similarly, animals are predicted to select habitats that best minimise the costs of disturbance relative to net energy gain (Gilliam and Fraser, 1987; Lima and Dill, 1990). Specifically, long-term intense disturbance stimuli are predicted to cause habitat shifts (where profitable alternatives exist) and/or avoidance of disturbed habitats (at the cost of reduced access to resources) (Frid and Dill, 2002).

Understanding how animals deal with human disturbance is critical for the effective management and conservation of any endangered species. The Moroccan High Commission for Water, Forests and Desertification Control (HCEFLCD), in collaboration with numerous non-governmental organisations (NGOs) and wildlife charities, published a Conservation Action Plan for the Barbary macaque in Morocco in 2012 (HCEFLCD, 2012). The three principal aims of this plan are 1) to restore suitable/optimal macaque habitat; 2) to reduce human pressure (including the reduction of human-macaque conflict); and 3) to control the poaching and illegal trade of macaques. In order to realise these aims it is essential to understand 1) how macaques use the fragmented and degraded habitat that is available to them; 2) how macaques respond to human activity and infrastructure in areas where the species overlap; and 3) how macaques are exposed, and made more vulnerable to, the threat of poaching.

To that end this study examines the responses of 5 wild Barbary macaque groups in INP to a range of human activities and infrastructure, at 2 distinct scales. The first research chapter compares pre-, during-, and post- human/dog-macaque encounter levels of escape, affiliative, and self-directed behaviours (behaviours that may serve as components of a coping strategy (Gustison, MacLarnon, Wiper, and Semple, 2012)) to determine whether different encounter types differentially affect macaque behavioural responses. I test the general hypotheses that a) macaques will use more coping behaviours during and/or immediately after human/dog encounters than before, and b) that different types of encounter will be associated with different types and magnitudes of coping behaviour. The second research chapter examines the behaviour-specific habitat use of macaques to determine whether and how different types of human activity and infrastructure influence habitat selection within home ranges. I test the general hypotheses that a) macaques will alter their habitat selection in response to human activity and infrastructure, and b) that different types of human activity and infrastructure will differentially affect macaque habitat selection.

Chapter 2: Human-macaque encounters in Ifrane National Park, Morocco: behavioural coping strategies of the Barbary macaque

2.1 Introduction

As human populations and resource requirements expand they inevitably encroach upon wildlife habitats. Human-wildlife encounters may occur more frequently as a result, particularly where resource conflict or wildlife tourism occur, or where wildlife habitat is used for human recreation (Hockings and McLennan, 2012; Hull et al., 2014; Reisland and Lambert, 2016). Human encounters/disturbances have the potential to alter the reproductive success, individual fitness, and population health of wild animals (Frid and Dill, 2002), and an increasing number of species, populations, and individual animals are being exposed to these consequences.

The way in which wildlife respond to human encounters depends on a combination of factors including: encounter frequency, duration, intensity, and type (Hockin et al., 1992; Wright et al., 2007); species-specific characteristics, such as degree of behavioural plasticity or perceptual range; and individual-specific attributes, such as temperament (degree of neophobia, for example) (Sol, Lapiedra, and González-Lagos, 2013). Individual animals should also evaluate the potential cost of an encounter with any potential benefit it may bring (Frid and Dill, 2002). For example, for crop-raiding olive baboons (*Papio hamadryas anubis*) in Nigeria the cost of being chased and attacked by farmers is outweighed by the benefits of increased access to calorie-dense food, e.g. a reduction in pathogen load and an increase in reproductive output (Warren, Higham, Maclarnon, and Ross, 2011).

Understanding the ways in which animals respond to and cope with different human encounters (and whether certain types of encounter impact them more than others) is an important conservation goal, particularly when the fate of many wildlife populations depends on their capacity to coexist with humans. Conservationists must often work with limited resources, so an understanding of how animals cope with different types of human encounter/conflict/disturbance may allow them to allocate these resources to the issues that warrant the most attention and/or the most immediate action. For example, yellow-bellied marmots (*Marmota flaviventris*) in the Upper East River Valley, Colorado, USA (an area used extensively for tourism) were found to exhibit a consistently stronger response (increased flight initiation distance) to pedestrians than to cyclists or motorists; the knowledge of which can be used to better manage the impact of those visitors (Li et al., 2011).

The efficient allocation of conservation resources is of particular concern when dealing with endangered species such as the Barbary macaque (*Macaca sylvanus*). The fragmented populations in the Middle Atlas Mountains of Morocco have been under increasing pressure for several decades, from human expansion (and the space and resource requirements that entails), unsustainable livestock practices, and unregulated wildlife tourism (Ciani et al., 2005; Ménard et al., 2014a; Ménard et al., 2014b; Van Lavieren, 2012). Morocco's growing population (c. 16 million to 34.3 million from 1970-2015) and gross national income per capita (a measure of the average annual income of a country's citizens) ($250 to $3040 from 1970-2015) (World Bank, 2016) have driven the human population's geographical and consumptive expansion into previously wild areas, ultimately restricting the availability of suitable macaque habitats. Many shepherds no longer abandon the high mountains in winter, instead remaining throughout, during which they may prune cedar trees to feed their livestock, further reducing the health and extent of the forest (Lamb, Damblon, and Maxted, 1991). The diversity and abundance of herbaceous and shrub resources has steadily declined as a result of overgrazing by sheep and goats (Ménard and Qarro, 1999), and the growth of unregulated tourist sites (that encourage and rely upon the feeding and residency of macaques) has progressed at a rapid pace. For example, within a busy (~1.85 km^2) area in Ifrane National Park, 3 heavily frequented tourist sites have been established within the last 20 years (L. Maréchal, personal communication, July 25, 2016).

One way in which animals can cope with the negative effects of human activity is by moving to a less disturbed area. The decision to do so or not will be determined by a complex combination of factors that include: the quality of the area already occupied, the quality of and distance to alternative areas, the relative risk of predation and/or competition in other areas, and the nature of any investment already made (e.g. attaining dominance status or establishing a defensible territory) (Gill, Norris, and Sutherland, 2001). However, animals without suitable habitat nearby and/or the ability to move (such as the Barbary macaque) will be forced to remain despite the disturbance. One possible response is for animals to alter their habitat use within fragments/home ranges to minimise human disturbance (see Chapter 3), but even if this strategy is successful they will still ultimately have to deal with more frequent human encounters. As such, animals must find ways to cope with these encounters, i.e. they must find ways of mitigating their costs whilst taking advantage of any benefits they can bring.

In doing so animals may choose (e.g. when accessing human food), or be compelled (e.g. when human activities and infrastructure overlap their home ranges) to expose themselves to close encounters with humans. Despite their differences, human encounters share the capacity to induce stress in the animals exposed to them (Maréchal et al. 2011; Rehnus et al., 2014; Shutt et al., 2014). Stress can be defined as "a perturbation of an organism's physiological and/or behavioural homeostasis as a result of exposure to certain events or situations (termed stressors)" (Novak, Hamel, Kelly, Dettmer, and Meyer, 2013, p. 136). Although perturbations may result from rewarding as well as aversive stimuli, the term is commonly used to describe the response to an aversive event or situation. While adaptive in the short term, chronically elevated stress levels can negatively impact animal health, reproductive success, and survival (Ellenberg, Mattern, Seddon, and Jorquera, 2006; Mumby et al., 2015; Sapolsky, 2004). As such it is essential that animals manage stress, including that induced by human encounters. One way in which they may do so is through the use of 'coping behaviours' (Gustison et al. 2012).

Various studies on a range of vertebrate species (including primates) have shown that certain behaviours (e.g. escape, affiliative, and self-directed/displacement behaviours) may help individuals to cope with stressful situations. For example, the most immediate (and effective) response to a stressful situation may be escape. Where possible an individual may reduce the impact of a stressor by moving away entirely, or in cases where an individual may also potentially profit from the stressor (e.g. during provisioning encounters), by maintaining control over proximity to the stressor (Weschler, 1995). For example, black howler monkeys (*Alouatta pigra*) in Belize move higher up in the forest canopy both as tourist numbers increase and as the intensity of the encounter increases (ranging from non-detection to physical contact) (Treves and Brandon, 2005). Similarly, pygmy marmosets (*Cebuella pygmaea*) in Ecuador preferentially use the upper canopy in response to increasing tourist pressure (De la Torre, Snowdon, and Bejarano, 2000).

Evidence for a coping function of affiliative behaviour can be found in a range of (predominantly mammalian) taxa, including rodents, cetaceans, birds, and primates (e.g. *Rattus norvegicus* – Albonetti and Farabollini, 1993; e.g. *Tursiops aduncus* – Connor, Mann, and Watson-Capps, 2006; e.g. *Corvus corax* - Stöwe et al., 2008; e.g. *Macaca sylvanus* - Shutt, MacLarnon, Heistermann, and Semple, 2007, respectively). When familiar animals are together they show reduced stress and fear symptoms in response to, and a better recovery from, stressful experiences; a phenomenon called 'social buffering' (Kikusui, Winslow, and Mori, 2006). These effects are more pronounced when positive social behaviours such as allogrooming, embracing, body-touching and contact-sitting occur (Aureli, 1997; Aureli, Van Schaik, and Van Hooff, 1989; Aureli and Yates, 2010; Boccia, Reite, and Laudenslager, 1989). For example, wild female chacma baboons (*Papio ursinus*) that lost a close relative to predation increased both grooming rate and number of grooming partners in the month following the event. The increased faecal cortisol levels that were evident following the loss returned to baseline levels during this period, an effect attributed to the increased rate of grooming and the expansion of grooming networks (Engh et al., 2006). Similarly, post-conflict reconciliation by means of affiliative behaviours (such as allogrooming, contact-sitting, and close approaches) and short affiliative gestures (such as teeth-chattering) reduces anxiety levels in a number of primate species, including olive baboons (Castles and Whiten, 1998), Japanese macaques (Kutsukake and Castles, 2001), and Barbary macaques (McFarland and Majolo, 2011).

Self-directed/displacement activities are thought to occur in situations in which an animal experiences motivational conflict or frustration (Anselme, 2008; McFarland, 1966; Tinbergen, 1952). The most commonly reported behaviours relate to body care, e.g. self-grooming or scratching (Troisi, 2002), and rates of self-scratching are commonly used as a measure of anxiety, particularly in primate studies (Castles, Whiten, and Aureli, 1999; Daniel, Dos Santos, and Vicente, 2008; Maestripieri, Schino, Aureli, & Troisi, 1992). Increases in the rate of self-directed behaviour have been observed in social situations likely to elicit anxiety, such as uncertainty about the assessment of rank (Schino, Maestripieri, Scucchi, and Turillazzi, 1990), about the risk of attack (Baker and Aureli, 1997; Polizzi di Sorrentino, Schino, Tiddi, and Aureli, 2012), or about the stability of post-conflict relations (Aureli and Van Schaik, 1991; Castles and Whiten, 1998). Pharmacological studies also support the use of self-directed behaviour rates as a measure of anxiety in primates, showing that rates increase in response to anxiogenic (anxiety inducing) drugs and decrease in response to anxiolytic (anxiety reducing) drugs (Maestripieri et al., 1992; Schino, Troisi, Perretta, and Monaco, 1991). Self-directed behaviour rates have also been used to quantify primate stress levels in response to human encounters, e.g. self-scratching rates among male Barbary macaques are positively related to the mean number of tourists present (Maréchal et al., 2011). Bwindi mountain gorillas (*Gorilla beringei beringei*) also show a significant increase in self-directed behaviours when in the presence of tourists (Muyambi, 2005), as do Sulawesi crested black macaques (*Macaca nigra*) (Paulus, 2009) and Tibetan macaques (*Macaca thibetana*) (Matheson et al., 2007).

In addition, several studies suggest that self-directed behaviours may serve to reduce the physiological stress response, possibly by initiating another sensory input to interfere with the original stressor (Maestripieri et al., 1992; Mason, 1991). For example, small-eared bushbabies (*Otolemur garnettii*) that engaged in more displacement activities (foot and chest rubbing) in a novel environment exhibited lower cortisol levels (the concentration of which is commonly used as an index of stress (O'connor, O'halloran, and Shanahan, 2000)) in response to restraint stress (Watson, Ward, Davis, and Stavisky, 1999). Similarly, human females that displayed higher rates of displacement activity during a stressful interview showed lower cardiac and parasympathetic disturbance symptoms during post-stress recovery (Pico-Alfonso et al., 2007). It has also been suggested that certain displacement activities (self-grooming, scratching, shaking, and yawning) in female olive baboons may be part of a behavioural coping strategy to reduce the physiological effects of stress (Highham, Maclarnon, Heistermann, Ross, and Semple, 2009).

It seems reasonable to suggest that more stressful situations will be associated with a more pronounced increase in the use of these coping behaviours than less stressful situations. As such the quantification and comparison of coping behaviours may offer insight into which types of encounter cause animals the most stress, and which therefore should be the focus of conservation efforts. This chapter examines the use of coping behaviours by 5 groups of wild Barbary macaques in Ifrane National Park in response to 5 different types of human/dog encounter (please refer to methods section 2.2.3 - Data Collection).

I test the general hypotheses that a) because human/dog encounters have the potential to induce stress in macaques, they will use more coping behaviours during and/or immediately after encounters than before, and b) that because different types of human/dog encounter pose different combinations of risk/reward, different types of encounter will be associated with different types and magnitudes of coping behaviour. I evaluate 3 predictions that test these hypotheses:

Prediction 1: If human/dog encounters induce stress in Barbary macaques, their use of escape behaviours will increase in association with those encounters. Specifically, I test whether:

1a) Macaques’ flight rate is higher during and/or after human/dog encounters than before.

1b) Macaques’ rate of tree ascension, and the proportion of time that macaques spend in the trees is higher during and/or after human/dog encounters than before.

1c) Different encounter types are associated with different magnitudes of change in macaque escape behaviour.

Prediction 2: If human/dog encounters induce stress in Barbary macaques, their use of affiliative behaviours will increase in association with those encounters. Specifically, I test whether:

2a) Macaques' rate of approaches to another individual, and the proportion of time macaques spend in close proximity to another individual (within a 1.5 m radial distance) is higher during and/or after human/dog encounters than before.

2b) Macaques approach more individuals (to within a 1.5 m radial distance) per hour during and/or after human/dog encounters than before.

2c) Macaques engage in more grooming bouts, and spend a greater proportion of time grooming with another individual during and/or after human/dog encounters than before.

2d) Macaques engage in grooming behaviour with more partners per hour during and/or after human/dog encounters than before.

2e) Macaques’ rate of short affiliative behaviours is higher during and/or after human/dog encounters than before.

2f) Macaques engage in short affiliative behaviours with more partners per hour during and/or after human/dog encounters than before.

2g) Different encounter types are associated with different magnitudes of change in macaque affiliative behaviour.

Prediction 3: If human/dog encounters induce stress in Barbary macaques, their use of displacement behaviours will increase in association with those encounters. Specifically, I test whether:

3a) Macaques' rate of self-scratching is higher during and/or after human/dog encounters than before.

3b) Macaques' frequency of self-grooming bouts, and the proportion of time macaques spend self-grooming is higher during and/or after human/dog encounters than before.

3c) Different encounter types are associated with different magnitudes of change in macaque displacement behaviour.

2.2 Methods

2.2.1 Study Area

This study was conducted in Ifrane National Park in the Middle Atlas Mountains of Morocco (33°25’N : 005°10’W), close to the city of Azrou (Figure 1). The park covers an area of 518 km^2 and ranges in elevation from 1400 to 2000 metres above sea level (m.a.s.l.) (Annuaire statistique régional Meknès-Tafilalet, 2006).

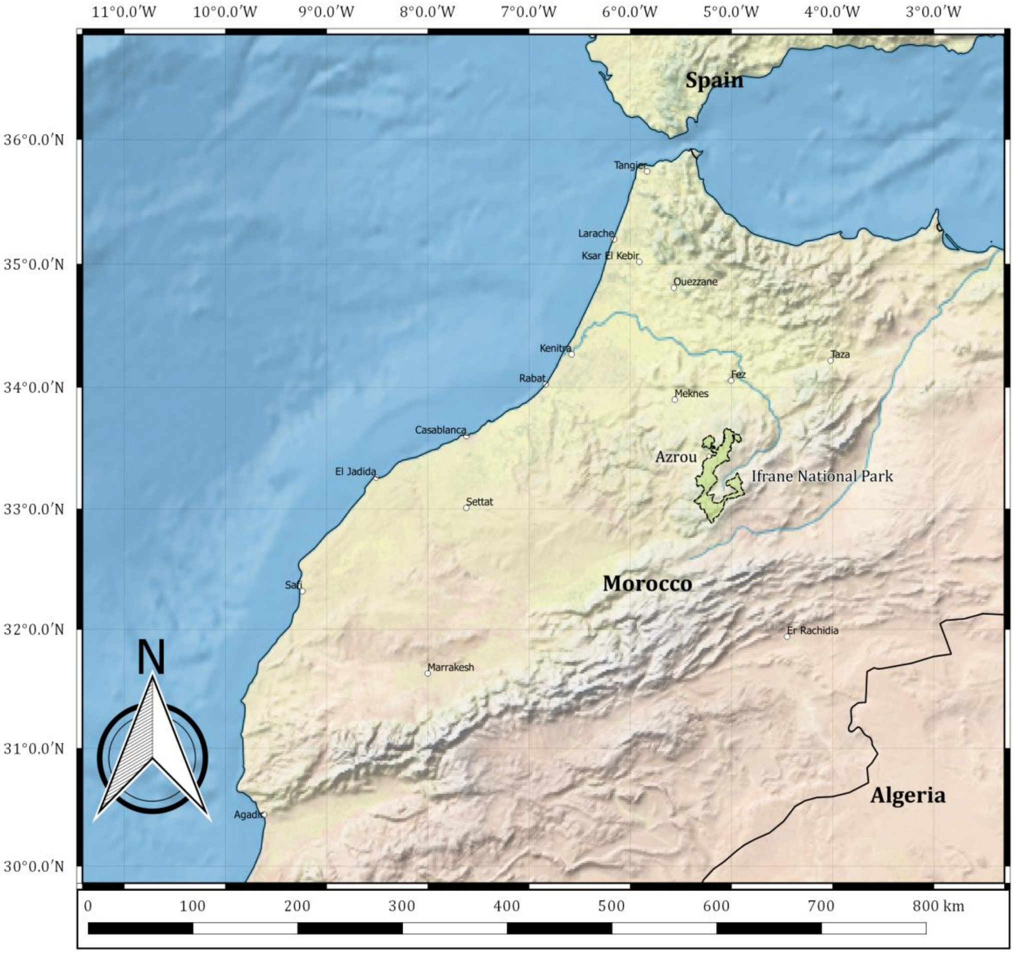

Figure 1. Map showing the location of Azrou and Ifrane National Park within Morocco. Basemap source: Natural Earth data (2016).

The study area (Figure 2) is largely covered by deciduous Atlas cedar and mixed oak (*Querces ilex* and *Querces faginea*) forest with patches of open scrubland. Annual temperatures vary from -7°C to +38°C (with snowfall over winter) (mean ± SE=15.95±0.13 °C per day); rainfall varies from 0 mm to 117 mm (mean ± SE=3.96±0.28 mm/d), and humidity from 0% to 100% (mean ± SE=57.53±0.38 % per day) (Majolo, McFarland, Young, and Qarro, 2013). The forest is inhabited by species that include: golden jackals (*Canis aureus*), domestic and feral dogs, red foxes (*Vulpes*

vulpes), genets (*Genetta genetta*), and several species of raptor (including the Bonelli's eagle (*Aquila fasciata*)), all of which are potential macaque predators (SENS, 2006).

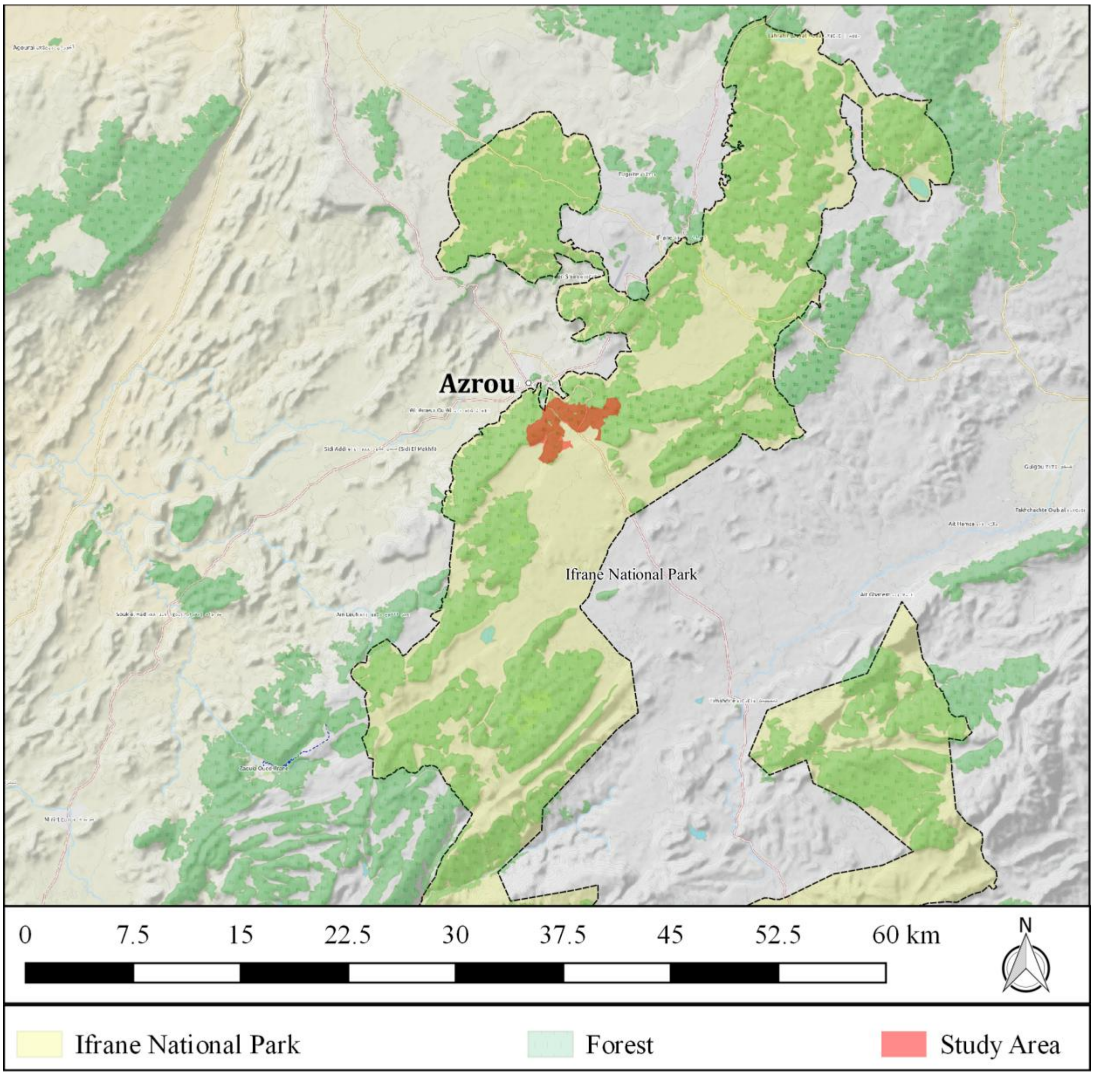

Figure 2. Map showing the location of the study area in relation to the city of Azrou. Basemap sources: OpenStreetMap (2016) and Natural Earth data (2016).

Permission to conduct the study was granted by the Haut Commisariat des Eaux et Forêts et à la Lutte Contre la Désertification of Morocco (The Moroccan High Commission for Water, Forests and Desertification Control).

2.2.2 Study Subjects

Data were collected on 54 adult and 17 subadult (between 3 and 4 years old (Ménard and Vallet, 1997)) monkeys from 5 wild groups of Barbary macaques; the Blue, Green, Purple, Red, and Yellow groups (Table 1). The groups were tolerant (defined by Bejder, Samuels, Whitehead, Finn, and Allen (2009) as an instantaneously observed state, as opposed to 'habituated', which refers to the repeated measurement of a longitudinal process) of researchers, and individuals were identified based on physical characteristics such as facial markings, scars, or peculiarities of body shape and size. Only monkeys in the Blue group were regularly provisioned by humans (although all groups did receive a variable degree of provisioning during the study, either from tourists (primarily the Blue and Yellow groups) or road users).

Table 1. Composition of macaque groups by sex and age class during the study period (January 2013 to April 2014). Numbers in brackets are the number of individuals that died or disappeared during the study period.

Group	Total number of individuals	Adult Males	Adult Females	Sub-adult Males	Sub-adult Females	Juveniles	Infants
Blue	35 (6)	8 (2)	7 (1)	3	2	11 (1)	4 (2)
Green	37 (4)	7	6	0	3	14	7 (4)
Purple	38 (5)	8 (2)	7 (1)	4	4	9 (1)	6 (1)
Red	13 (0)	4	3	0	0	3	3
Yellow	12 (1)	3	2	1	0	4	2 (1)

Macaque home ranges were determined using the kernel density estimate (KDE) method, a nonparametric technique for estimating the utilisation distribution of an individual or group based on a random sample of location data (Worton, 1989). Global positioning system (GPS) readings were taken every 60 minutes at the estimated centre of the group using a variety of Garmin handheld GPS devices (all of similar specification to the Garmin etrex Summit HC). The centre of the group was estimated as the point in the middle of an imaginary ellipse ‘drawn’ around all visible group members.

Home range data were analysed in ArcGIS 9.3.1 (Environmental Systems Research Institute) using the Hawth’s Analysis Tools – Kernel Density Estimator extension, allowing the tool to choose the most appropriate smoothing factor via least-squares cross-validation (Seaman and Powell, 1996; Worton 1989). 95% and 50% isopleths were generated for each group (Figure 3). Locations within the 95% isopleth represent the majority of the area used by a group (minus outliers or exploratory movements) and those within the 50% isopleth represent the core area of activity (Fashing et al., 2007; Kruse et al., 2001). All 5 groups’ 95% KDE home ranges (hereafter ‘home ranges’) overlapped with at least one other (Table 2), and each group’s home range included at least one type of human structure. Human activity within the study area was concentrated around 2 tourist sites, 2 water treatment plants, 2 roads (along which are numerous picnic spots and clearings), a complex of livestock stables, a small farm, and the herding routes of shepherds that use these structures (Figure 4).

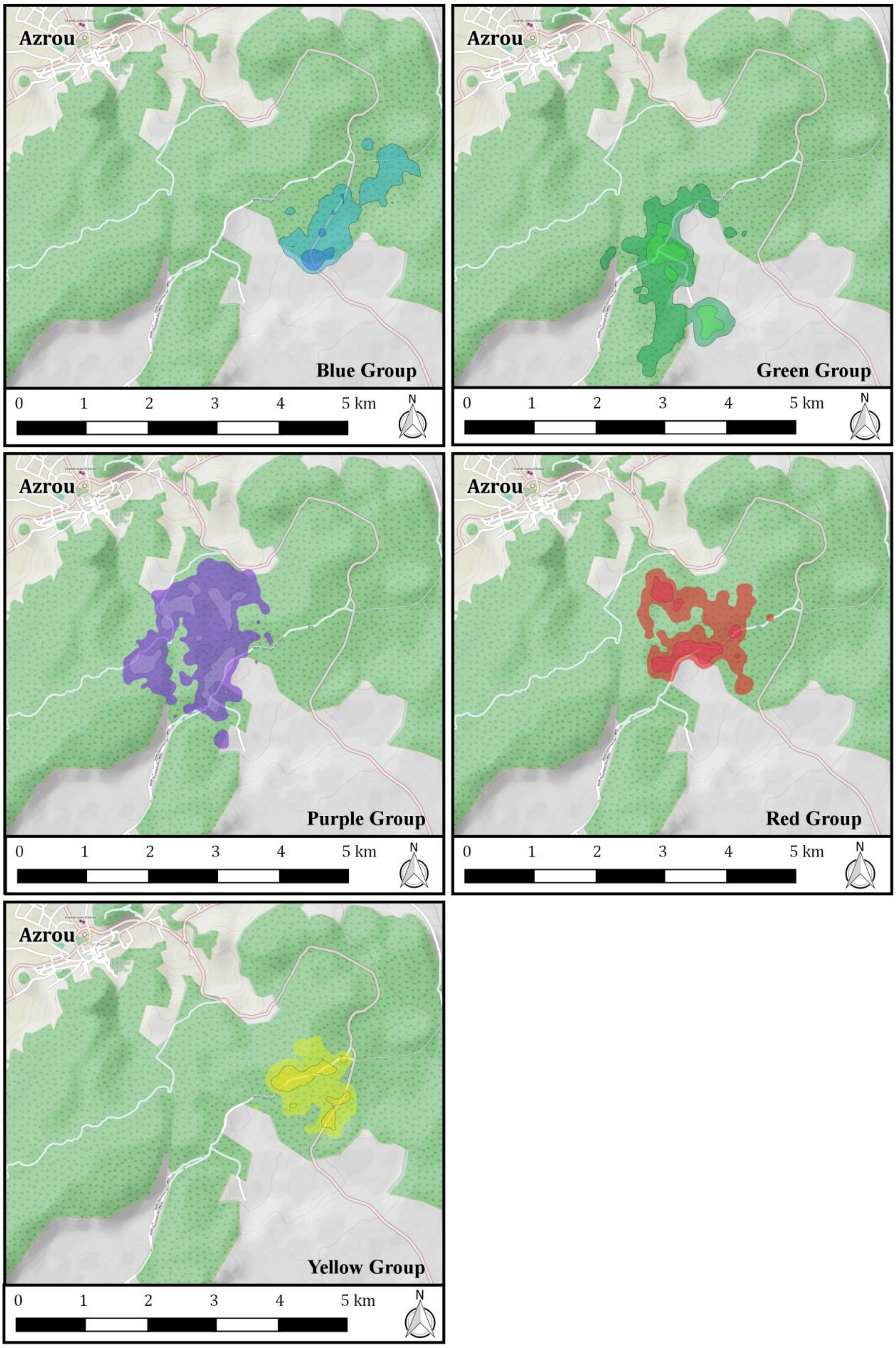

Figure 3. Maps showing the home ranges of the 5 study groups. The light coloured, outer polygons represent 95% KDE isopleths and the dark, inner polygons represent 50% KDE isopleths. Basemap sources: OpenStreetMap (2016) and Natural Earth data (2016).

Table 2. Home range area and overlap of study groups.

Group	Home range area (km^2)		
	Total (95% isopleth)	Core (50% isopleth)	Overlap (total)
Blue	1.93	0.18	0.64 (33.2%)
Green	3.09	0.57	1.20 (38.8%)
Purple	4.26	0.97	2.01 (47.2%)
Red	2.63	0.56	2.13 (81.0%)
Yellow	1.89	0.47	1.1 (58.2%)

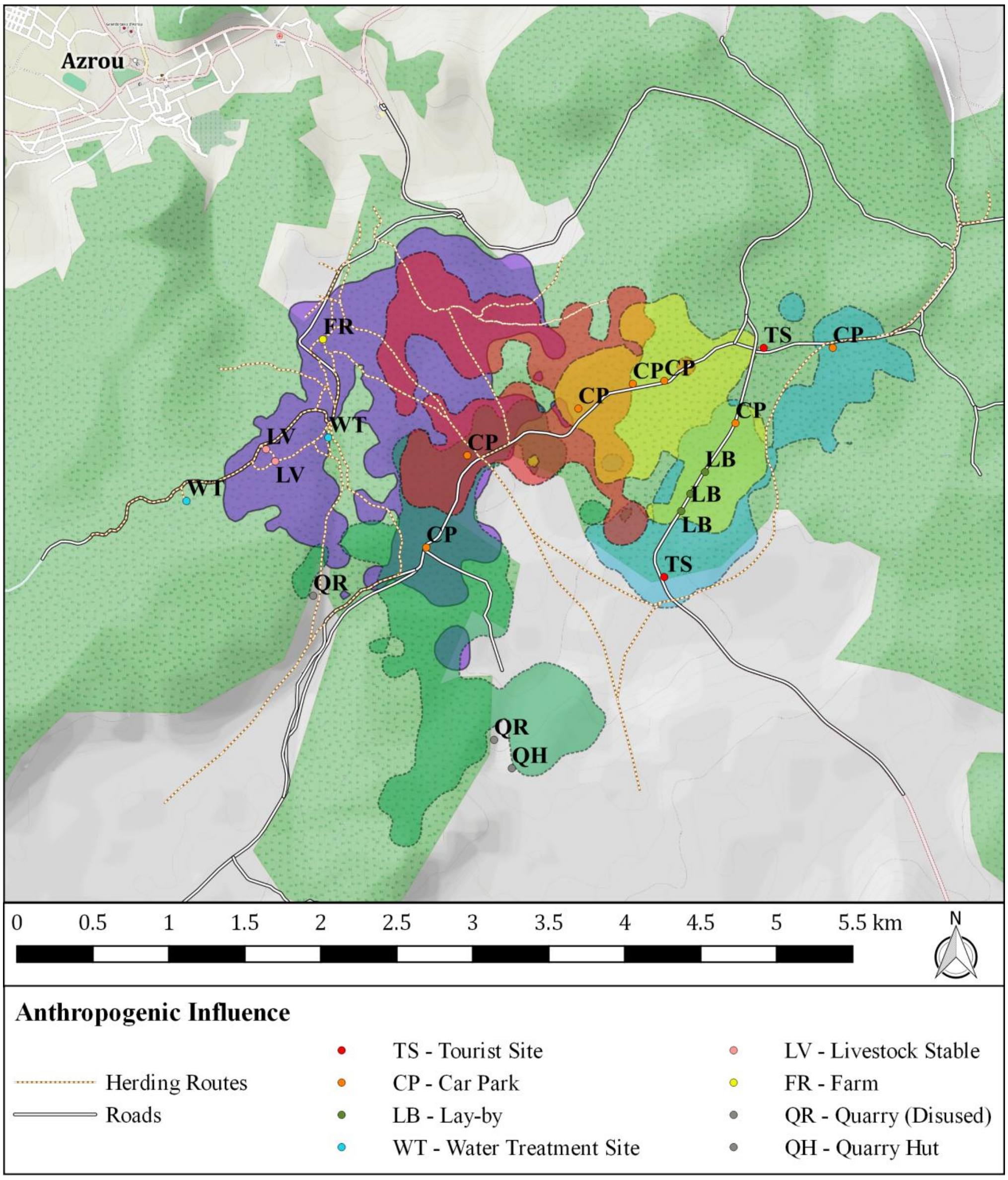

Figure 4. Map showing the overlapping home ranges of the study groups and the location of anthropogenic structures within the study area. Basemap sources: OpenStreetMap (2016) and Natural Earth data (2016)

2.2.3 Data Collection

The study groups were monitored daily between 06:00 and 19:00 (mean daily observation hours ± SE: 9.20±0.19), visibility permitting, from June 2013 to April 2014. Behavioural data were collected during 30 minute focal observations, using ‘continuous all occurrences focal animal sampling (Altmann, 1974) (referred to hereafter as ‘focals’), yielding a total of 556 hours of data over 1126 focals (Table 3). The majority of these focals (75.1%) were undisturbed by humans/dogs, i.e. the full 30 minute duration elapsed without any ‘disturbers’ (defined here as humans, livestock, and/or dogs) coming within 20 m of the group. Because no during- or post-encounter behaviour was recorded, these focals were unsuitable for use in this analysis. However, if an anthropogenic encounter did occur during a focal observation, another 30 minutes were added to the sampling time and the encounter was eligible for inclusion in this analysis. Twenty metres was chosen as the engagement/disengagement distance following several months of preliminary observations, the results of which indicated that macaques began to respond (by directing vigilance and/or alarm calling) to ‘disturbers’ at approximately this range.

If an encounter occurred within 3 minutes of the focal observation start time, the focal was excluded from analysis on the grounds that a pre-encounter duration comprising 10% or less of the total baseline focal duration (30 minutes) could be a) unrepresentative of pre-encounter behaviour, and b) ‘contaminated’; i.e. if the focal individual detected an encounter before the observer, data recorded as pre-encounter may have actually been during-encounter. For the same reason, all data recorded in the minute prior to the recorded start time of an encounter were also excluded from analysis, i.e. to limit the possibility of including ‘contaminated’ behavioural data. An encounter was recorded as over when no more disturbers were within 20 m of the group. One hundred and four focals (totalling 70 hours 35 minutes) recorded the behaviour of the focal animal before, during, and/or after an anthropogenic encounter and were suitable for use in the following analyses.

Table 3. Mean focal observation time and standard error per individual (by group, sex, and age-class) for all observations. NA represents unpopulated sex/age-classes.

Group	Data Collection	Mean focal observation time per individual (hours ± SE)				
		Total	Adult Males	Adult Females	Sub-adult Males	Sub-adult Females
Blue	May 31, 2013 – April 21, 2014	5.7±0.6	7.0±0.3	7.3±0.6	0.4±0.06	0.6±0.5
Green	June 6, 2013 – April 21, 2014	9.0±0.7	9.9±0.4	10.4±0.3	NA	1.9±0.4
Purple	May 31, 2013 – April 21, 2014	9.7±1.1	13.1±0.3	13.7±0.3	1.3±0.2	3.3±1.1
Red	June 8, 2013 - August 15, 2013	3.7±0.4	3.2±0.2	4.3±0.8	NA	NA
Yellow	June 1, 2013 – April 12, 2014	14.9±1.9	15.0±0.9	18.9±0.2	6.3±0.0	NA

The order in which individuals were sampled within each group was randomised within each 24 hour (or for large groups, 48 hour) block of observation time, with an attempt made to sample every individual in the group at least once during this time. All focal data were collected by 6 research assistants, 2 colleagues (engaged in a different but concurrent study) and I, using handheld PC's (HP iPAQ 111) loaded with Pendragon Forms software, version 5.1.2 (Pendragon Software Corporation). Parallel focal observation trials (using my data as the standard) were conducted to check for interobserver reliability. A minimum agreement score of 80% was required (and in all cases achieved) before an observer's data were included in the study.

Following an ethogram (Table 4) focal data were used to quantify rates (events per hour (separate events distinguished by a 10 second gap)) and proportions (time observed in behavioural state divided by total observation time (separate states also distinguished by a 10 second gap) of escape, affiliative, and self-directed behaviours. Anthropogenic encounters were also recorded as states. Because the stress-relieving effect of social-buffering is influenced by the number of partners involved (Coe, Franklin, Smith, and Levine, 1982; Stanton, Patterson, and Levine, 1985), the identity of all affiliative partners was recorded and the proportion of time spent in multiple-partner affiliative behaviours (specifically allogrooming and proximity) was allowed to exceed 1.

Table 4. Ethogram of behavioural data collected; after Maréchal (2015).

Behaviour Class	**Behaviour**		**Definition**
Escape	Tree ascension		The monkey enters a tree. Tree defined as any woody plant on a single main stem or trunk that exceeds a height of 1 m.
	Flight		The monkey moves away from a stimulus at high speed, usually in response to a threat or aggressive action.
Affiliative	Approach and Proximity		The monkey approaches (or is approached by) another to within a radial distance of 1.5 m.
	Allogrooming		The monkey cleans the surface of another's body (using its fingers or mouth) by licking, nibbling, and picking with the fingers.
	Short affiliative behaviours	Teeth-chattering	The monkey's lips and cheeks are retracted to show the teeth and usually the gums. The mouth opens and closes rapidly with teeth contacting teeth, often with the tongue sticking out. The eyebrows and scalp may also be pulled up and the ears flattened against the head.
		Lip-smacking	The monkey's lips are pursed and the lower jaw is moved up and down rapidly and rhythmically. The jaw may be thrust upward. The mouth may be slightly open with the tongue moving back and forth. The eyebrows and scalp may also be pulled up and the ears flattened against the head.
		Sandwich	An infant monkey is simultaneously handled by two other monkeys; often associated with teeth-chattering.
		Embrace	Two monkeys grab each other by the arms and/or legs and feet. Can be ventral-ventral or ventral-dorsal.
		Touch body	The monkey briefly touches another with its hand. Distinguished from an aggressive or sexual touch by force, velocity, and context.
		Contact-sitting	Two or more monkeys are sitting still in body contact i.e. touching with any part of the body. No other behaviour, such as grooming, is occurring.
Displacement	Self-scratching		The monkey uses its fingers to scrape its own body.
	Self-grooming		The monkey cleans the surface of its body (using its fingers or mouth) by licking, nibbling, and picking with the fingers.

For each encounter the following information was recorded: the location of the encounter (using a handheld GPS unit), the type of disturber (e.g. shepherd, tourist, forager with dog), and a running total of the number of disturbers (in order to yield a 'maximum disturber number'). Encounters were first classified according to whether humans and/or dogs were present, and whether they were using the park for work or recreation. This decision was based on observations made by myself and a team of research assistants that when human-macaque encounters occurred, if the humans were working (e.g. shepherds driving livestock or foragers collecting wood) they would largely ignore the macaques, if they saw them at all. These encounters were usually brief, lasting only as long as it took for the humans to pass. On the contrary, if the humans were using the park for recreation (e.g. picnicking, sightseeing, or exercising) they would very often attempt some form of interaction with the macaques, and these encounters usually lasted much longer than those with ‘working humans’ (mean duration of encounter; work: 14.6±1.6 min, recreation: 23.2±0.7 min). Given these broad differences in human behaviour towards the macaques it is reasonable to suggest that the macaques may perceive these encounters differently. For example, although not all encounters with ‘recreational humans’ included provisioning, many did (29.6%, n=192), a fact that may be reflected in the frequent approaches made to ‘recreational humans’ in comparison to the almost total absence of approach behaviour towards ‘working humans’, who rarely if ever provisioned the macaques (1.7%, n=56). Because of the potential for provisioning, encounters with ‘recreational humans’ may have an attractive quality for the macaques, whilst encounters with working humans do not. In addition many ‘working humans’ were accompanied by dogs (dogs were present during 37.5% (n=56) of encounters with ‘working humans’ and only 6.7% (n=192) of encounters with ‘recreational humans’), which given that they represent a predatory threat to the macaques (Lyon, 2012; Maréchal, 2015; personal observation) may have also changed their perception of these encounters. For these reasons 5 categories of encounter were defined:

- **‘Work’**: Encounters with humans using the park for work purposes. This includes shepherds, foragers, forest guards, charcoal production teams, and logging crews.
- **‘Work-Dog’**: As ‘Work’ when dogs are present.
- **‘Dog-Solo’**: Encounters with unaccompanied dogs.
- **‘Recreation’**: Encounters with humans using the park for recreational purposes. This includes picnickers, sightseers, joggers, campers, and wildlife tourists.
- **‘Recreation-Provisioned’**: As ‘Recreation’ when food is given to the macaques.

2.2.4 Data Analysis

To examine the relationship between escape, affiliative, and self-directed behaviours, and the occurrence and type of human/dog encounters, the rates and proportions of pre-encounter behaviours were compared to those recorded during and after encounters. A series of generalised linear mixed models (GLMMs) with Gamma error distributions and log links were used (Tables 5 and 6). GLMMs allow the simultaneous analysis of multiple independent variables whilst controlling for the non-independence of repeated sampling by treating experimental units (individual macaques before, during, and after encounters) as random factors (Zuur, Ieno, Walker, Saveliev, and Smith, 2009).

Table 5. Description of the dependent variables included in GLMM's.

Behaviour Class	Variable	Description
Escape	Tree ascension rate	Number of ground to tree ascensions per hour
	Tree proportion	Proportion of observation time in the trees
	Flight rate	Number of flight events per hour
Affiliative	Approach rate	Number of approaches per hour
	Proximity proportion	Proportion of observation time in close proximity to another individual
	Approach/proximity partners	Number of different partners approached per hour
	Short affiliative behaviour rate	Number of short affiliative behaviours per hour
	Short affiliative behaviour partners	Number of different short affiliative behaviour partners per hour
	Grooming bouts	Number of grooming bouts per hour
	Grooming proportion	Proportion of observation time grooming
	Grooming partners	Number of different grooming partners per hour
Displacement	Self-scratching rate	Number of self-scratches per hour
	Self-grooming bouts	Number of self-grooming bouts per hour
	Self-grooming proportion	Proportion of observation time self-grooming

Table 6. Description of the independent variables included in GLMM's.

	Variable	Type	Levels	Description
Main factors	Condition	Categorical	3	Pre, during, and post-encounter
	Encounter type	Categorical	5	Work, Work-Dog, Dog-Solo, Recreation, Recreation-Provisioned
	Condition * Encounter type	Categorical	15	Pre * Work, Work-Dog, Dog-Solo, Recreation, Recreation-Provisioned
				During * Work, Work-Dog, Dog-Solo, Recreation, Recreation-Provisioned
				Post * Work, Work-Dog, Dog-Solo, Recreation, Recreation-Provisioned
	Group size	Discrete	NA	Number of individuals in the group at time of sampling
	Maximum number of disturbers	Discrete	NA	Maximum number of disturbers recorded during an encounter
	Home range position	Categorical	2	Core (within 50% isopleth), Outer (outwith 50% isopleth)
Random factors	Focal sample (nested within Subject)	Categorical	104	Unique code identifying each sequence of pre, during, and post encounter observations
	Subject	Categorical	50	Unique code identifying each individual macaque

Condition, encounter type, and the two-way interaction term, *condition * encounter type* were included as the principal explanatory variables. Given the similarity between wildlife responses to nonlethal anthropogenic disturbance and predation risk (Frid and Dill, 2002), *group size* was included as an explanatory variable to detect any differences in response associated with the dilution (Hamilton, 1971) or increased vigilance effects (Van Schaik, Van Noordwijk, Warsono, and Sutriono, 1983), and to control for the differing number of potential affiliative partners within each group (Lehmann, Korstjens, and Dunbar, 2007). *Maximum number of disturbers* and *home range position* were included as explanatory variables to investigate the respective roles of disturber group size (Aguilar-Melo et al., 2013; Treves and Brandon, 2005) and geographical familiarity (Clarke et al., 1993; Isbell, Cheney, and Seyfarth, 1990) on response behaviours. Each focal sample was assigned a unique code which was included as a random factor (nested within the identity of each individual macaque) in order to control for the repeated sampling of individuals both within and across focal samples. Identically constructed models were used to examine the relationship between the number of affiliative (grooming, approach, and short affiliative behaviour) partners and the occurrence and type of human/dog encounters.

Models were fitted using the 'glmer' command of the 'lme4' package (Bates, 2010) within the R platform (Version 3.2.3) (R Core Team 2015) and estimated using Laplace approximation as recommended by Bolker et al. (2009). All models were validated following the procedures of Bolker et al. (2009) and Thiele and Markussen (2012): histograms of the raw observations were examined to ensure the appropriate choice of error distribution, residual plots were used to assess the appropriateness of the link function and model fit, and normal quantile plots of the random effects were examined. In all cases no obvious deviations from the required expectations were observed. Models were also checked for evidence of collinearity between predictors using variance inflation factors ('vif' function in the package 'car' (Fox and Weisberg 2011)) as recommended by Barr, Levy, Scheepers, and Tily (2013).

Each behavioural response was treated as a dependent variable and analysed using a separate model. The significance of each full model was assessed by comparison to a corresponding null model (i.e. an intercept-only model with no independent variables) using a likelihood ratio test ('anova' function in the 'stats' package (R Core Team 2015) with test set to "Chisq") (Zuur et al., 2009) and only statistically significant models were examined further. The significance of the individual fixed effects (independent variables) of significant models was determined based on the Wald *t*-statistics and *p*-values provided by ‘glmer’. In order to avoid the problems associated with stepwise model selection (Whittingham, Stephens, Bradbury, and Freckleton, 2006) (specifically the possibility that statistically non-significant fixed effects may still influence the model) the significance of all fixed effects was tested using full models. The use of identical models for each dependent variable also allowed for a simple comparison of behavioural responses. All statistical tests were two-tailed with α set to 0.05.

2.3 Results

2.3.1 Escape behaviour

There was a marked increase in the use of escape behaviours by macaques in response to both human and dog encounters. Flight rates were significantly higher during ‘Work’, ‘Recreation-Provisioned’, and ‘Dog-Solo’ encounters than before (Figure 5; see Appendix A - Table 1 for full model results), and increased as the maximum number of disturbers increased (however this result should be treated with caution as the positive relationship between flight rate and maximum number of disturbers was largely driven by the presence of a single outlier) (Figure 6; Appendix A - Table 1). Tree ascension rates (and the proportion of time spent in the trees) were significantly higher during ‘Work-Dog’ encounters and both during and after ‘Dog-Solo’ encounters than before (Figures 7 and 8; Appendix A - Table 1), and the proportion of time macaques spent in the trees was also significantly higher after ‘Recreation-Provisioned’ encounters than before (Figure 8; Appendix A - Table 1).

2.3.2 Affiliative behaviour

Macaques approached each other at a significantly higher rate after ‘Work’ encounters, and a significantly lower rate after ‘Recreation-Provisioned’ encounters than before (Figure 9; Appendix A - Table 2). No other significant changes in approach rate (or the number of different partners approached) were observed, however the proportion of time spent in close proximity to another individual was significantly greater both during and after ‘Work-Dog’ encounters than before, and significantly lower during ‘Work’ encounters than before (Figure 10; Appendix A - Table 2).

By comparison, macaque grooming behaviour changed little in response to human/dog encounters. Grooming bout frequency was significantly lower after ‘Recreation-Provisioned’ encounters than before (Figure 11; Appendix A - Table 3), however the proportion of time spent grooming was significantly higher both during and after ‘Work-Dog’ encounters (Figure 12; Appendix A - Table 3). No significant change in the number of grooming partners was observed (Appendix A - Table 4), but the proportion of time that macaques spent grooming (averaged over all encounter types and conditions) was significantly greater when in the core, rather than the outer regions of their home ranges (Figure 13; Appendix A - Table 3).

Several significant changes in the use of short affiliative behaviours were observed in response to human/dog encounters. Both the rate of short affiliative behaviours and the number of partners involved were significantly lower during ‘Work’ encounters than before (Figures 14 and 15; Appendix A - Tables 2 and 4). However both of these measures (short affiliative behaviour rate and number of partners) were significantly higher during ‘Recreation-Provisioned’ encounters and after ‘Work-Dog’ encounters than before (Figures 14 and 15; Appendix A - Tables 2 and 4).

2.3.3 Self-directed behaviour

Macaque self-scratching rates were significantly higher during ‘Recreation-Provisioned’ encounters than before, and after ‘Dog-Solo’ encounters than before (Figure 16; Appendix A - Table 5). However this was the only significant change in the use of self-directed behaviour in response to human encounters; neither the frequency of self-grooming bouts nor the proportion of time spent self-grooming differed significantly between conditions (Appendix A - Table 5).

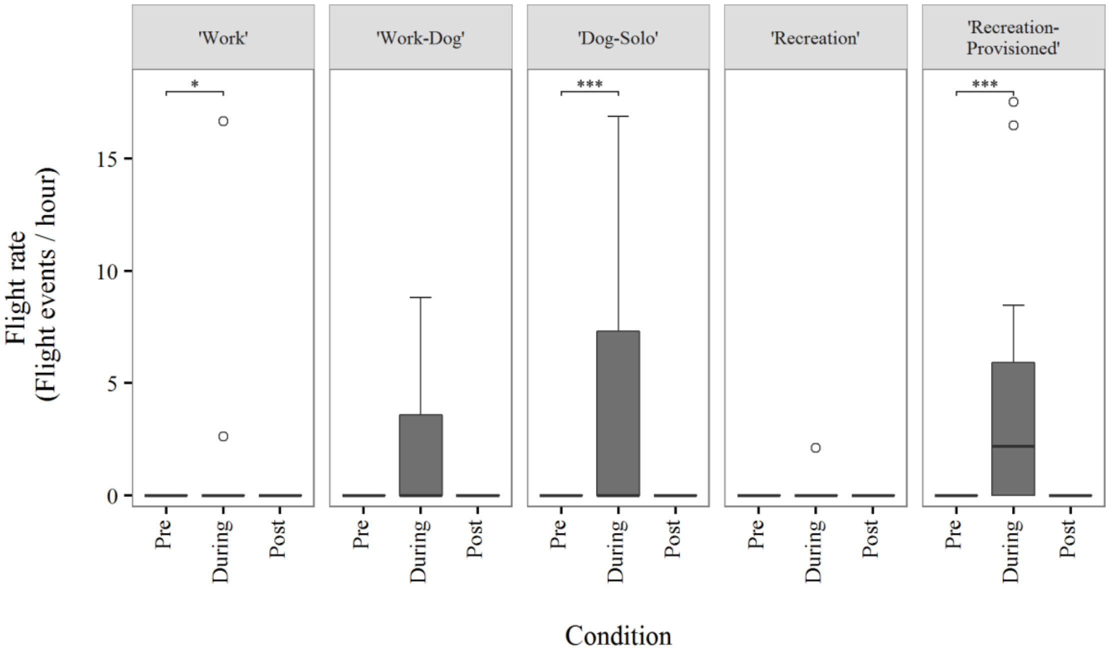

Figure 5. Flight rate of macaques before, during, and after different types of human/dog encounter. Each box encompasses the 25th through 75th percentiles, with the median represented by an interior line. Whiskers denote 10th and 90th percentiles. Open circles indicate outliers. Asterisks indicate statistically significant differences between conditions. * P<0.05; **P<0.01; ***P<0.001.

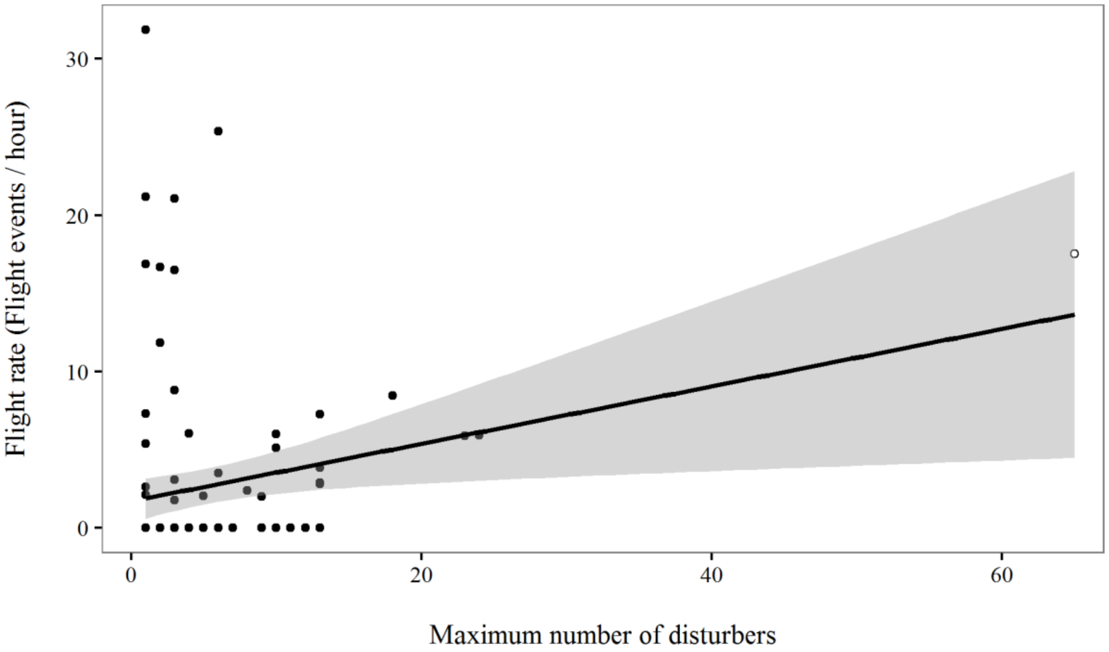

Figure 6. Flight rate of macaques in relation to the maximum number of disturbers present during an encounter. Data are pooled across encounter types. Shaded area represents the 95% confidence region for the regression fit. This result should be treated with caution as the positive relationship between flight rate and maximum number of disturbers is largely driven by the presence of a single outlier (indicated by an open circle).

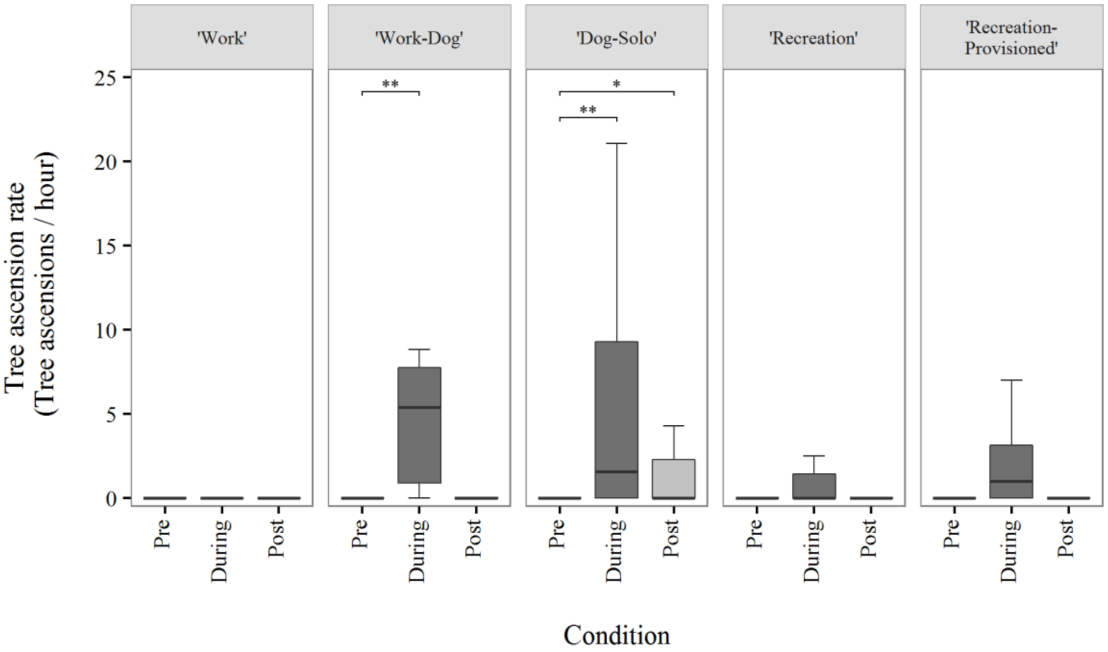

Figure 7. Tree ascension rate of macaques before, during, and after different types of human/dog encounter. Each box encompasses the 25th through 75th percentiles, with the median represented by an interior line. Whiskers denote 10th and 90th percentiles. Asterisks indicate statistically significant differences between conditions. * P<0.05; **P<0.01; ***P<0.001.

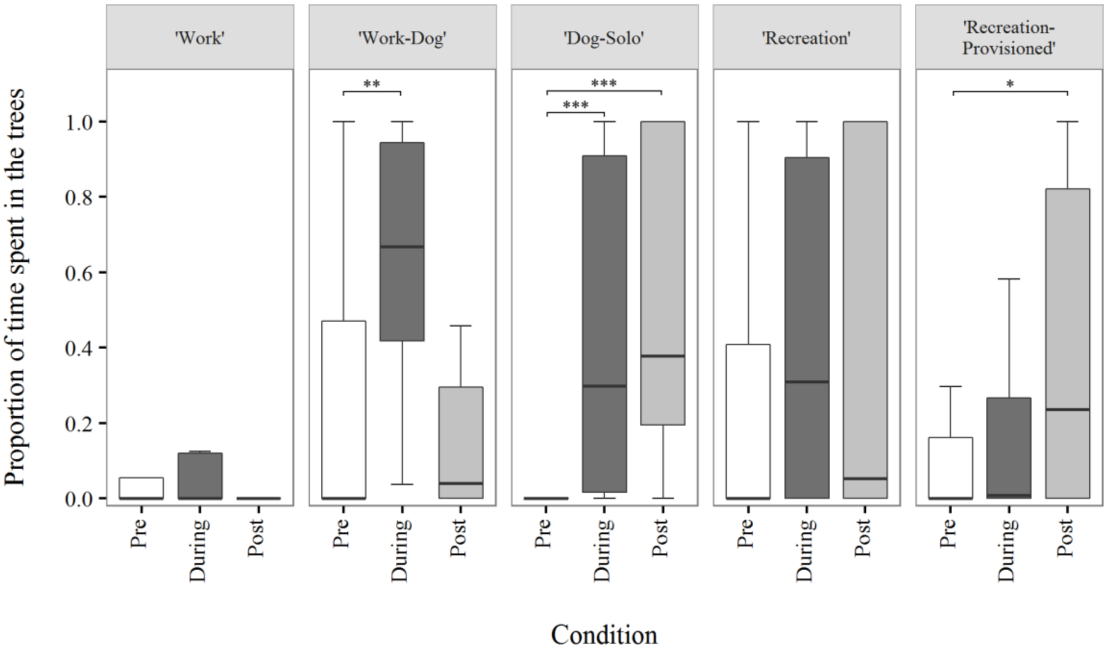

Figure 8. Proportion of time spent in trees before, during, and after different types of human/dog encounter. Each box encompasses the 25th through 75th percentiles, with the median represented by an interior line. Whiskers denote 10th and 90th percentiles. Asterisks indicate statistically significant differences between conditions. * P<0.05; **P<0.01; ***P<0.001.

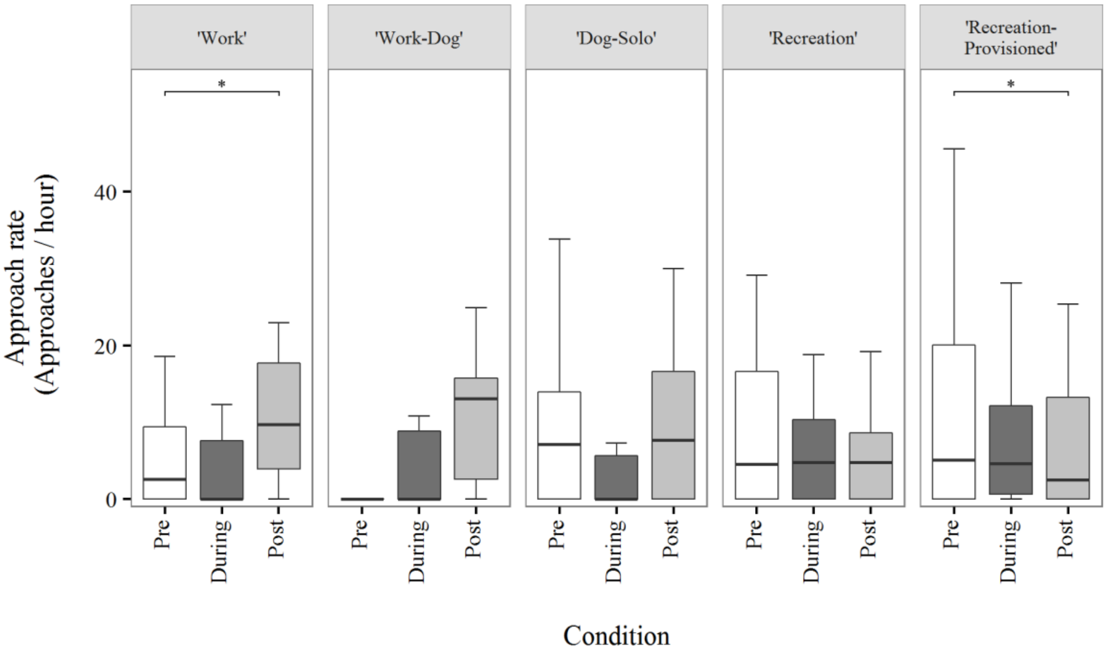

Figure 9. Approach rate of macaques (to within 1.5 m of another individual), before, during, and after human/dog encounters. Each box encompasses the 25th through 75th percentiles, with the median represented by an interior line. Whiskers denote 10th and 90th percentiles. Asterisks indicate statistically significant differences between conditions. * P<0.05; **P<0.01; ***P<0.001.

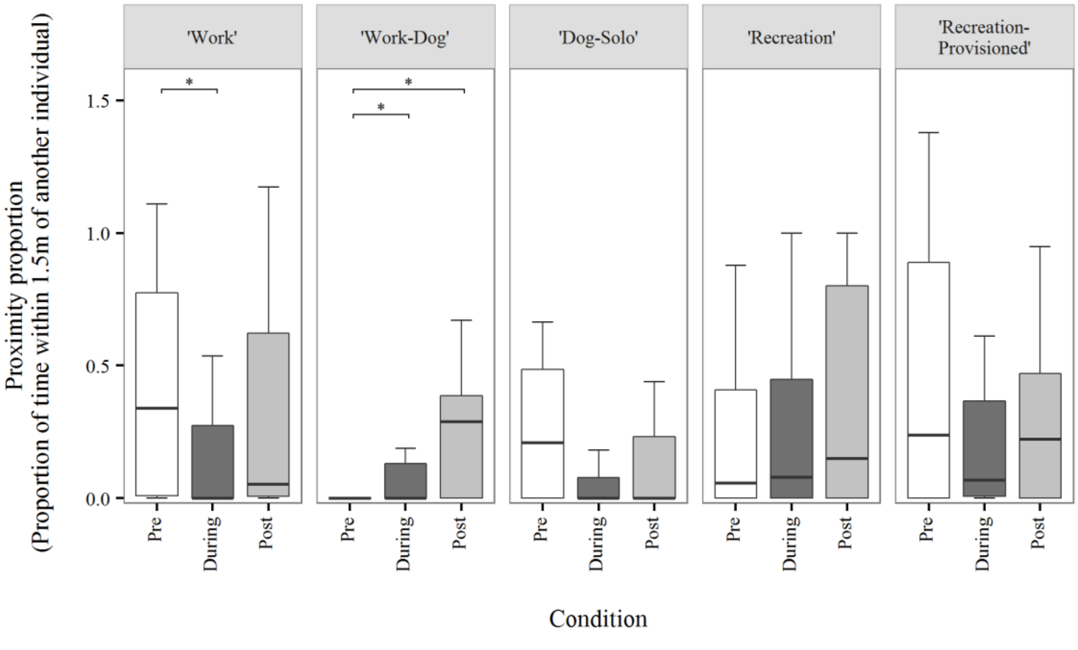

Figure 10. Proportion of time macaques spent in close proximity (within 1.5 m) to another individual before, during, and after human/dog encounters. Each box encompasses the 25th through 75th percentiles, with the median represented by an interior line. Whiskers denote 10th and 90th percentiles. Asterisks indicate statistically significant differences between conditions. * P<0.05; **P<0.01; ***P<0.001.

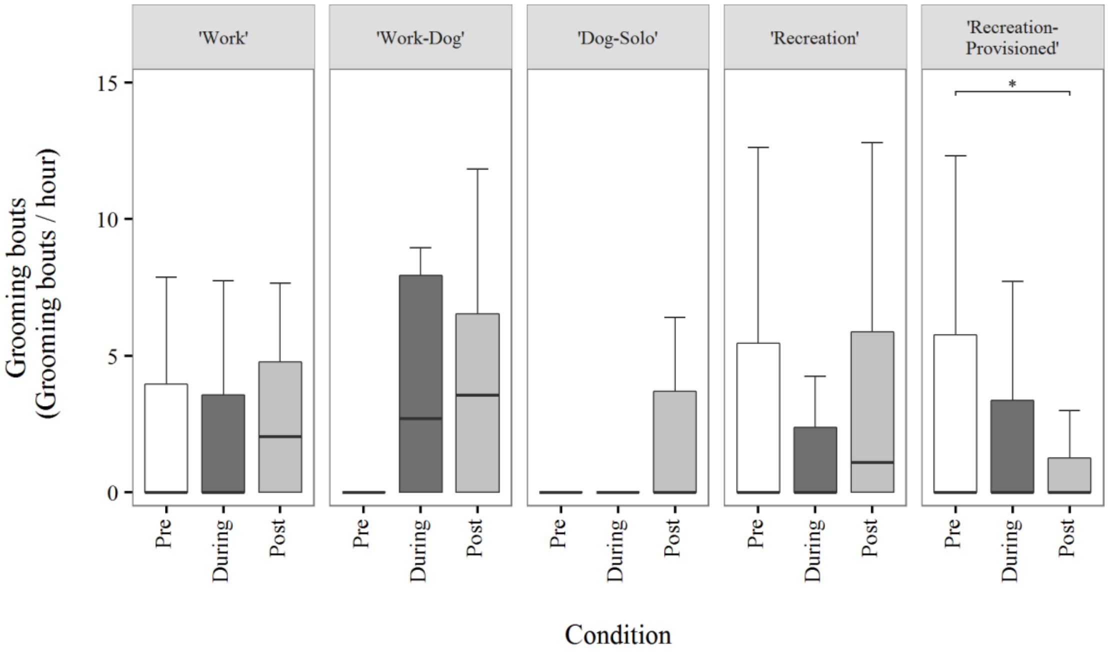

Figure 11. Frequency of grooming bouts (bouts per hour) before, during, and after different types of human/dog encounter. Each box encompasses the 25th through 75th percentiles, with the median represented by an interior line. Whiskers denote 10th and 90th percentiles. Asterisks indicate statistically significant differences between conditions. * P<0.05; **P<0.01; ***P<0.001.

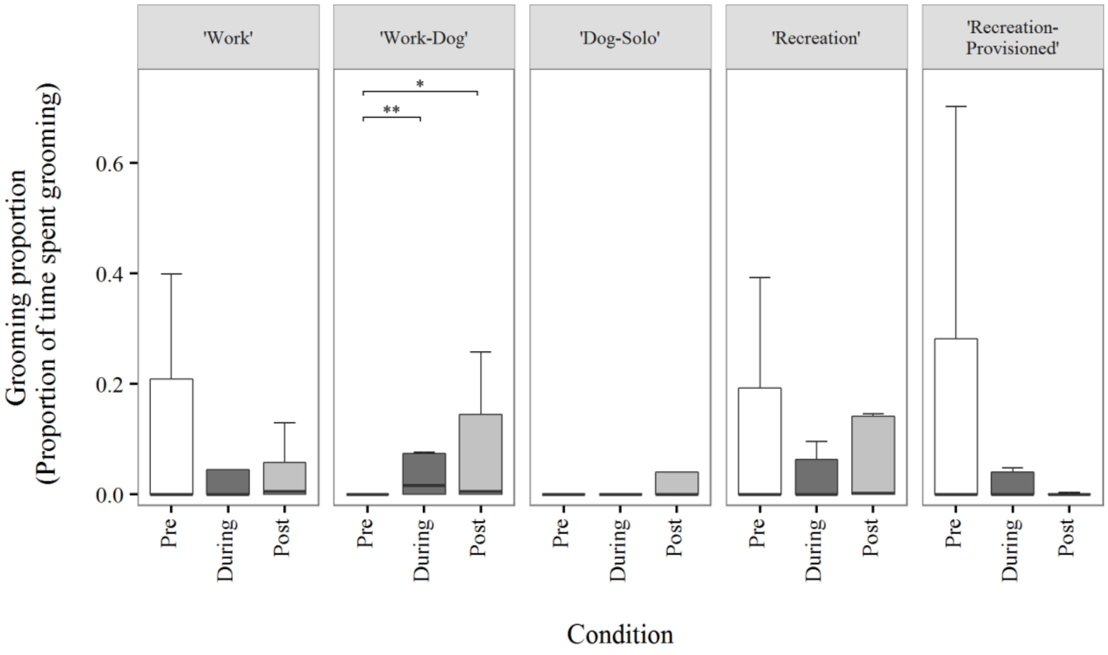

Figure 12. Proportion of time spent grooming before, during, and after different types of human/dog encounter. Each box encompasses the 25th through 75th percentiles, with the median represented by an interior line. Whiskers denote 10th and 90th percentiles. Asterisks indicate statistically significant differences between conditions. * P<0.05; **P<0.01; ***P<0.001.

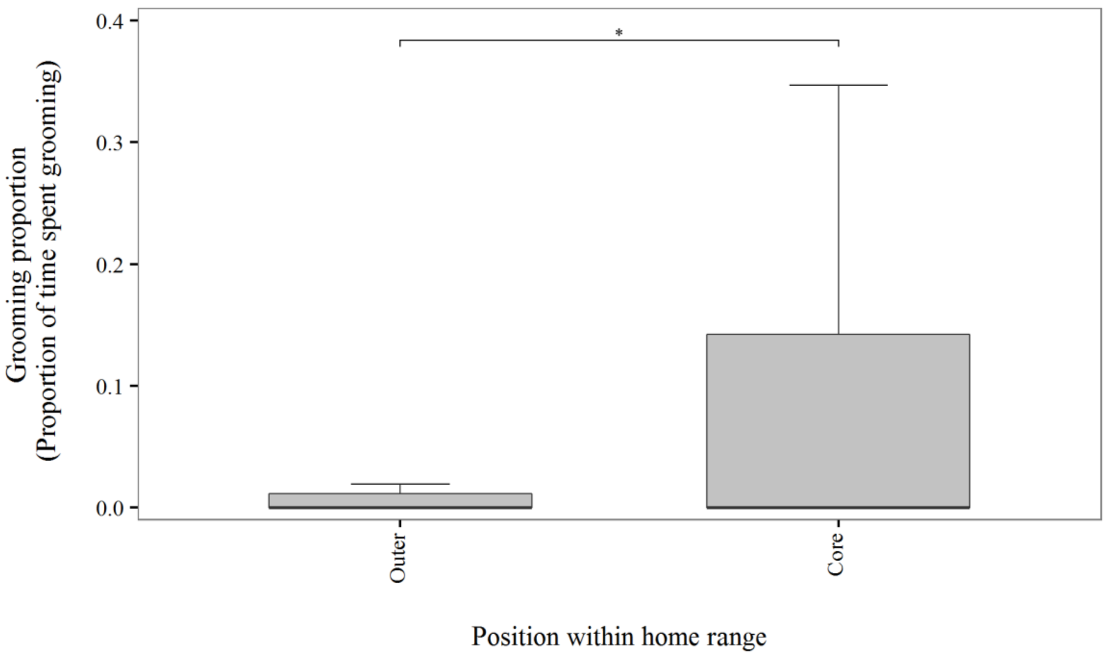

Figure 13. Proportion of time macaques spent grooming in the outer (95% KDE) and core (50% KDE) regions of home ranges. Data are pooled across encounter types and conditions. Each box encompasses the 25th through 75th percentiles, with the median represented by an interior line. Whiskers denote 10th and 90th percentiles. Asterisks indicate statistically significant differences between conditions. * P<0.05; **P<0.01; ***P<0.001.

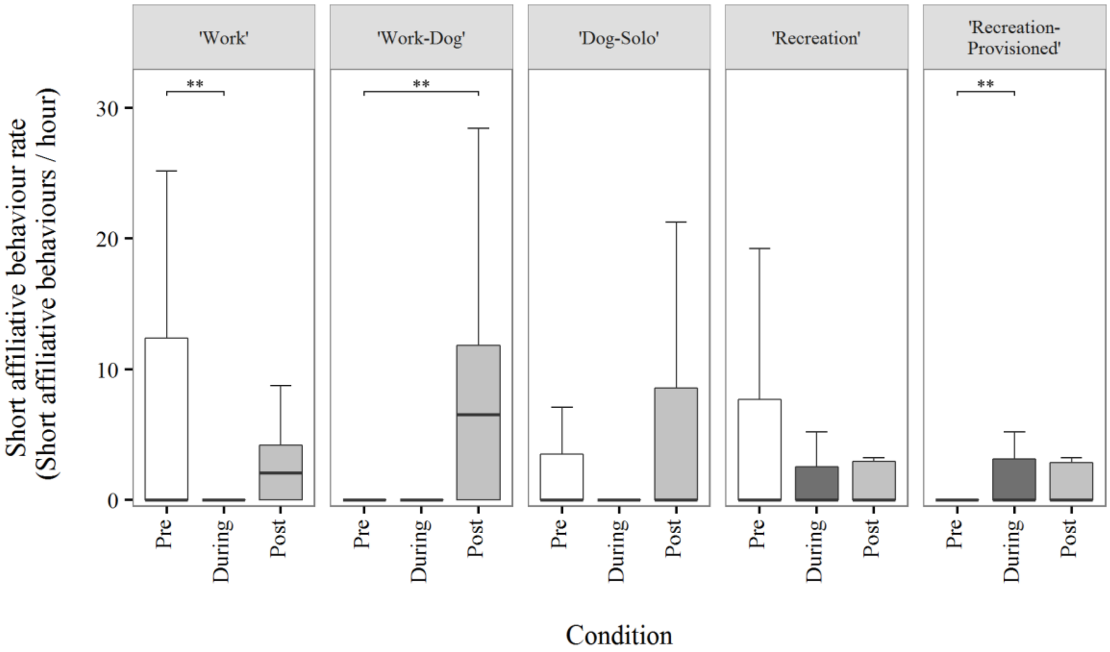

Figure 14. Short affiliative behaviour rate of macaques before, during, and after different types of human/dog encounter. Each box encompasses the 25th through 75th percentiles, with the median represented by an interior line. Whiskers denote 10th and 90th percentiles. Asterisks indicate statistically significant differences between conditions. * P<0.05; **P<0.01; ***P<0.001.

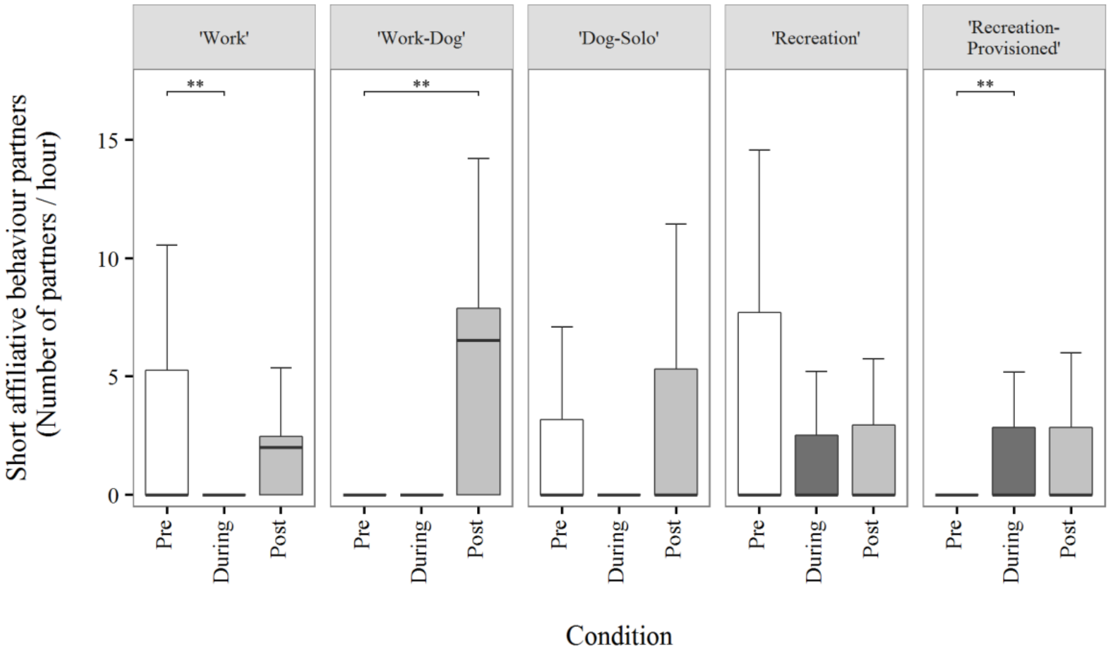

Figure 15. Number of short affiliative partners (per hour) before, during, and after different types of human/dog encounter. Each box encompasses the 25th through 75th percentiles, with the median represented by an interior line. Whiskers denote 10th and 90th percentiles. Asterisks indicate statistically significant differences between conditions. * P<0.05; **P<0.01; ***P<0.001.

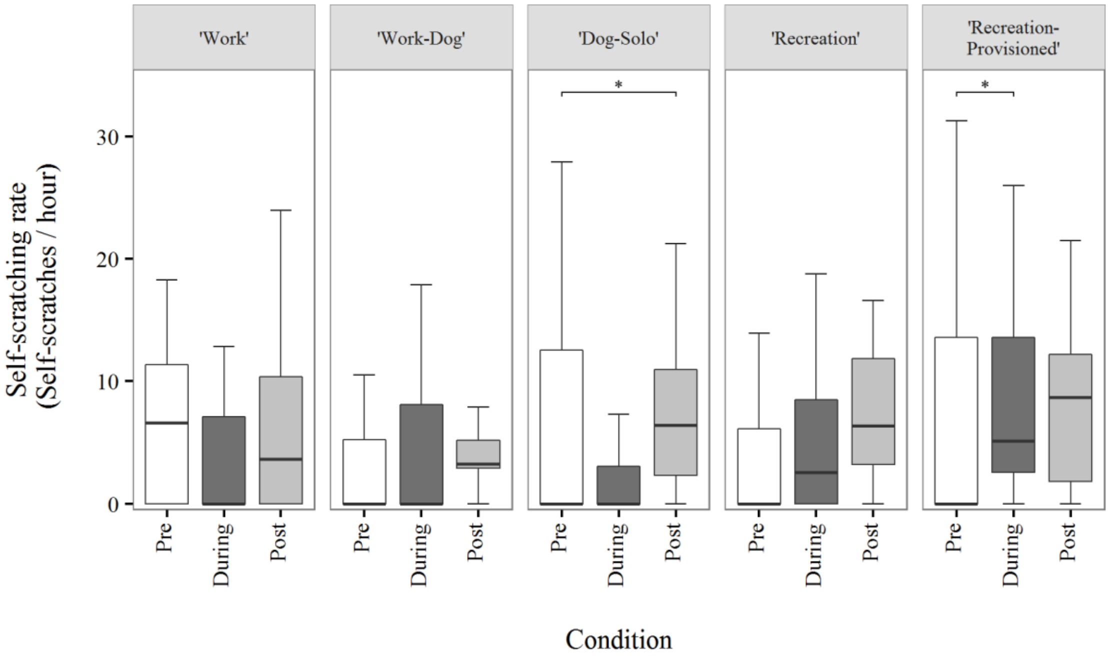

Figure 16. Self-scratching rate of macaques before, during, and after human/dog encounters. Each box encompasses the 25th through 75th percentiles, with the median represented by an interior line. Whiskers denote 10th and 90th percentiles. Asterisks indicate statistically significant differences between conditions. * P<0.05; **P<0.01; ***P<0.001.

Table 7. Summary of predictions, rationale, and support provided by this study. Predictions test the general hypothesis that Barbary macaques use more coping behaviours during and/or immediately after human encounters than before.

Prediction	Rationale	Prediction Details	Supported
1. Escape behaviour will increase during and/or after human encounters	The impact of a stressor may be reduced when an individual has control over their proximity to it	Flight rate higher during and/or after human encounters than before	Yes
		Tree ascension rate higher during and/or after human encounters than before	Yes
		Proportion of time in trees higher during and/or after human encounters than before	Yes
	Certain encounter types may be more stressful for macaques than others	Different encounter types associated with different changes in escape behaviour	Yes
2. Affiliative behaviour will increase during and/or after human encounters	Close proximity to familiar conspecifics may alleviate the physiological stress response (social buffering)	Approach rate higher during and/or after human encounters than before	Yes
		Proportion of time in close proximity to another individual higher during and/or after human encounters than before	Yes
		Number of individuals approached higher during and/or after human encounters than before	No
	The stress relieving effects of social buffering are more pronounced when positive contact behaviours occur	Grooming bout frequency higher during and/or after human encounters than before	Yes
		Proportion of time spent grooming higher during and/or after human encounters than before	Yes
		Number of grooming partners higher during and/or after human encounters than before	No
	Short affiliative behaviours may alleviate the physiological stress response	Short affiliative behaviour rate higher during and/or after human encounters than before	Yes
		Number of short affiliative behaviours partners higher during and/or after human encounters than before	Yes
	Certain encounter types may be more stressful for macaques than others	Different encounter types associated with different changes in affiliative behaviour	Yes
3. Displacement behaviour will increase during and/or after human encounters	Displacement behaviours may reflect and/or alleviate the physiological stress response	Self-scratching rate higher during and/or after human encounters than before	Yes
		Self-grooming frequency higher during and/or after human encounters than before	No
		Proportion of time spent self-grooming higher during and/or after human encounters than before	No
	Certain encounter types may be more stressful for macaques than others	Different encounter types associated with different changes in displacement behaviour	Yes

Table 8. Summary of results by encounter type. Plus/minus symbols indicate a statistically significant increase/decrease in behaviour compared to pre-encounter levels. 'S.A.B.' refers to short affiliative behaviours; 'Pre' refers to pre-encounter, 'Dur' to during-encounter, and 'Post' to post-encounter period.

Behaviour		**Encounter type**									
		'Work'		**'Work-Dog'**		**'Dog-Solo'**		**'Recreation'**		**'Recreation-Provisioned'**	
		Dur	**Post**	**Dur**	**Post**	**Dur**	**Post**	**Dur**	**Post**	**Dur**	**Post**
Escape	Tree ascension			+		+	+				
	Tree proportion			+		+	+				+
	Flee	+				+				+	
Affiliative	Approach		+								-
	Proximity proportion	-		+	+						
	Proximity partners										
	S.A.B.	-			+					+	
	S.A.B. partners	-			+					+	
	Grooming bouts										-
	Grooming proportion			+	+						
	Grooming partners										
Displacement	Self-scratch						+			+	
	Self-grooming bouts										
	Self-grooming proportion										

2.4 Discussion

As predicted, Barbary macaques showed a general increase in the use of coping behaviours in association with human/dog encounters (Tables 7 and 8). With the exception of 'Recreation' encounters without provisioning (which elicited no significant changes in coping behaviour) macaques made extensive use of escape behaviours both during and after all types of human/dog encounter. Affiliative behaviours both increased and decreased depending on encounter type whilst self-directed behaviours increased in association with 'Recreation-Provisioned' and 'Dog-Solo' encounters. These results support the general hypotheses that a) macaques will use more coping behaviours during and/or immediately after human/dog encounters than before, and b) that different types of encounter will be associated with different types and magnitudes of coping behaviour. This highlights the importance of examining wildlife responses to multiple types of encounter/stressor simultaneously (using data from the same population, and ideally individuals) when evaluating the impact of human-wildlife encounters.

As indicated by Table 8, 2 broadly consistent 'response profiles' were observed; the first in association with encounters that involved/potentially involved dogs, and the second with encounters that involved provisioning by humans. These may be best understood as a response by macaques to the potential costs and benefits associated with specific encounter types.

2.4.1 Potentially threatening encounters: 'Work', 'Work-Dog', 'Dog-Solo'

2.4.1.1 Escape behaviours

In response to encounters that involved the potential threat of predation by dogs, macaques consistently responded with increased levels of escape behaviour. When dogs were present ('Work-Dog' and 'Dog-Solo' encounters) macaques fled to the trees and generally remained there at least until the encounter was over. When dogs were not present ('Work' encounters) macaques also fled, but generally remained on the ground, suggesting that the primary driver of tree ascension was the presence of dogs.

Domestic/working and feral dogs represent a significant threat to wildlife (Young et al., 2011) and are capable of catching and killing macaques (Anderson, 1986). Various studies have reported dog attacks on Barbary macaques; in the Rif mountains (Mehlman, 1989), the Middle Atlas (Deag and Crook, 1971), and at this study site (Maréchal, 2015).

Indeed the body of an adult male from the Purple group was found, surrounded and mauled by dogs, during the course of this study. Although the precise cause of death could not be confirmed the corpse was found at the base of an isolated tree, near a stable complex inhabited by sheep dogs. Given the potentially lethal cost of a dog attack it is unsurprising that macaques fled to the trees and spent an increased proportion of time there in response to dog encounters. This is a common primate response to terrestrial predators. Both redfronted lemurs (*Eulemur fulvus rufus*) and white sifakas (*Propithecus verreauxi verreauxi*) consistently respond to experimental playbacks of terrestrial predator alarm calls by climbing up into the trees (Fichtel and Kappeler, 2002), as do white-faced capuchin monkeys (*Cebus capucinus*) in response to actual terrestrial predator (including human) alarm calls (Fichtel, Perry, and Gros-Louis, 2005).

Given the energetic and lost opportunity costs associated with escape behaviour it is notable that in addition to spending an increased proportion of time in the trees during ‘Work-Dog’ and ‘Dog-Solo’ encounters, macaques also did so after ‘Dog-Solo’ encounters had ended. This may be linked to the different behavioural patterns of accompanied and unaccompanied dogs. Accompanied (i.e. working) dogs would typically follow the humans they were with, moving away from the macaques as the humans did. They were in general a) less likely to approach and harass macaques than unaccompanied dogs, b) identified earlier by macaques (because a large group of livestock usually approached with them), and c) much slower to approach macaques, if they did at all (personal observations). Unaccompanied dogs however would consistently approach macaques at high speed, prompting a rapid flight response up into the trees. They were also more likely to remain in the vicinity of the macaques for longer periods of time, and often departed and returned in quick succession. As such although the data collection protocol indicated that an encounter was over when a disturber was 20 m away from the group, this distance could be (and in the case of unaccompanied dogs, generally was) covered very quickly by dogs. It may be that the macaques have a different perception than observers of when these types of potentially threatening encounters are actually ‘over’ and so exercise caution by remaining in the trees for some time after the recorded end point. By remaining in the trees macaques may also improve their ability to detect the dogs’ possible return. For example, patas monkeys (*Erythrocebus patas*) take advantage of tall trees to detect predators (including domestic dogs), giving significantly more alarm calls when in taller than average trees (Enstam and Isbell, 2004).

2.4.1.2 Affiliative behaviours

The differences in accompanied and unaccompanied dog behaviour may also help to explain why no increase in affiliative behaviours was observed during ‘Dog-Solo’ encounters (in contrast to the broad increase observed in association with ‘Work-Dog’ encounters). Because lone dogs generally approached faster than working dogs it may not have been possible for macaques to ascend trees together, or to risk covering the distance to an already occupied tree in order to associate with other individuals during ‘Dog-Solo’ encounters. However, although this might explain why no increase in approach and/or grooming behaviours (i.e. contact behaviours) was observed during ‘Dog-Solo’ encounters, it does not adequately explain why no increase in short affiliative behaviours (i.e. largely gestural behaviours) was observed either. It is possible that as seen in red-fronted lemurs, and lesser bamboo lemurs (*Hapalemur griseus*), macaques adopt a cryptic anti-predator strategy in response to ‘Dog-Solo’ encounters by restricting their activity levels (Karpanty and Wright, 2007).However if this were the case we might expect to see a significant reduction in affiliative (and indeed all other) behaviours, rather than simply an absence of their increase. The failure to observe a reduction in activity during ‘Dog-Solo’ encounters may however be attributable to methodological shortcomings, i.e. despite the establishment of a 20 m engagement radius, and the removal of data 1 minute prior to the start of a disturbance, given the potential approach speed of lone dogs it is possible that the macaques were aware of their presence before the observers and had adopted a cryptic strategy in advance of any disturbance being recorded, hence the failure to observe a decrease in activity. Indeed, if this is the case then it might explain why no increase in any affiliative (or displacement) behaviour was observed during ‘Dog-Solo’ encounters, whilst an increase in affiliative behaviours was observed during ‘Work-Dog’ encounters. Because accompanied dogs are generally following humans/livestock they are less likely to stay and harass the macaques even if they do notice them. Unaccompanied dogs however are unconstrained by ‘work responsibilities’ and so may approach the macaques at much greater speed, and stay and harass them for longer periods of time. As such the best strategy when encountering unaccompanied dogs may be for macaques to try and avoid detection in the first place.

If macaques do adopt a cryptic anti-predator strategy it may be that the reduction in affiliative behaviours observed during ‘Work’ encounters is in fact the true reflection of this strategy. Only once the potential threat has passed do macaques then seek out close contact with other individuals in order to alleviate the stress response (an increase in approach rate was also observed after ‘Work’ encounters). Several primate species utilise a selective cryptic anti-predator strategy in response to particular types of predator. For example, female Campbell’s monkeys (*Cercopithecus campbelli*) remain cryptic in response to eagles but join males in approaching leopards (*Panthera pardus*) (Ouattara, Lemasson, and Zuberbühler, 2009). And male Diana monkeys (*Cercopithecus diana diana*) react to pursuit-type predators (i.e. those that search for prey using acoustic cues, specifically chimpanzees (*Pan troglodytes*) and humans) and not surprise-type predators (i.e. those that stalk and ambush prey, specifically crowned hawk eagles (*Stepanoaetus coronatus*) and leopards) by remaining temporarily cryptic (Zuberbühler, Noë, and Seyfarth, 1997).

The broad increase in affiliative behaviours observed both during and after ‘Work-Dog’ encounters however more clearly supports the general hypotheses that human encounters have the potential to induce stress in macaques, and that they use coping behaviours to alleviate this stress. The time spent in close proximity to other individuals, and the time spent grooming increased during (and after) encounters, and short affiliative behaviours (and the number of partners) also increased after ‘Work-Dog’ encounters. A similar effect is observed in ringtailed lemurs (*Lemur catta*) where individuals engage in grooming behaviour following encounters with predatory raptors (Sauther, 1989). The increase in short affiliative behaviours (and number of partners) after ‘Work-Dog’ encounters may perform a similar function but on a wider scale. Whilst grooming and/or close proximity may be an effective way to relieve anxiety following a stressful encounter, both are largely restricted to 2-3 individuals at a time. The exchange of short affiliative behaviours however can occur with multiple group members almost simultaneously, over larger distances, whilst grooming for example continues uninterrupted. This may serve to alleviate tension on a group-wide scale, a supposition supported by the observation that the number of partners engaged in short affiliative behaviours also increased after ‘Work-Dog’ encounters.

The variable use of affiliative behaviours in response to potentially threatening encounters merits further attention and could benefit from a more detailed categorisation of ‘working human’ encounters according to exactly which type of disturbing stimuli is involved e.g. shepherds, foragers, forest guards, logging crews etc., rather than as ‘Work’/‘Work-Dog’ only. However for reasons of sample size I was unable to split the categories in this way. In addition, my personal observations suggest that macaques not only respond differently to certain types of 'working human' but may also recognise and respond differently (based on prior experience) to certain individuals, an ability that has been tentatively demonstrated in both rhesus macaques (*Macaca mulatta*) and chimpanzees (Keating and Keating, 1993; Martin-Malivel and Okada, 2007).

In trying to understand the variable use of affiliative behaviours between 'Work', 'Work-Dog', and 'Dog-Solo' encounters a final possibility warrants consideration. Despite the slower approach speed and reduced tendency of 'working dogs' to give chase, macaques may perceive 'Work-Dog' encounters as more stressful than 'Dog-Solo' encounters. Whilst unaccompanied dogs are generally more aggressive towards macaques, unlike humans they are unable to climb trees or to throw rocks. Although it was rare, during the course of the study I observed 3 human-macaque encounters in which (1) a small group (n=3) of shepherds, (2) a larger group (n=5) of foragers, and (3) a lone forest-guard (individuals employed by the state to protect and monitor the health of the flora and fauna in INP) encouraged their dogs to chase groups of macaques up into the trees, after which they proceeded to climb those trees (up to heights of approximately 25 m) in an attempt to capture isolated juvenile and infant macaques (cases 1 and 2 only). When this failed they catapulted and/or threw rocks and sticks, presumably in the hope of dislodging macaques from the relative safety of the trees (cases 1, 2, and 3). It may be therefore that 'Work-Dog' encounters actually represent a more potent, dual threat to macaques. They may have to contend with the threat of predation by dogs on the ground and a predator capable of climbing trees and throwing missiles. This may account for the large increase in affiliative behaviours associated with 'Work-Dog' encounters (as the stress induced is presumably greater). Given the long history of humans removing young macaques from the Middle Atlas (often using dogs to isolate them up trees) for the exotic pet/tourism industry (Ménard et al., 2014a; Van Lavieren and Wich, 2009) it is possible that macaque groups are equally as wary of encounters with both humans and dogs, as dogs alone. This may be particularly true if, as hypothesised above, macaques can recognise individual humans. This explanation however appears to be incompatible with the cryptic response-to-predation hypothesis detailed above. If 'Work-Dog' encounters represent a greater threat to macaques than either 'Work' or 'Dog-Solo' encounters, a similar cryptic response during 'Work-Dog' encounters should be expected.

2.4.1.3 Self-directed behaviours

The absence of any increase in self-directed behaviours in association with 'Work' and 'Work-Dog' encounters is particularly surprising. The cryptic response hypothesis might account for the absence during 'Work' and 'Dog-Solo' encounters (i.e. no increase in self-directed behaviour was observed because macaques are attempting to avoid detection), but it does not adequately explain the absence in association with 'Work-Dog' encounters (given that other (affiliative) behaviours increased) . However, if macaques do respond to lone dogs with a cryptic anti-predator strategy it may explain/contribute to the observed increase in self-scratching observed after 'Dog-Solo' encounters. If the encounter induced a stress response that could not be buffered during the event (because the encounter escalated quickly, left individuals in relative isolation, and/or triggered a cryptic response) this frustrated desire/unresolved anxiety may have been manifested in increased self-directed behaviour after the event (Schino, Scucchi, Maestripieri, and Turillazzi, 1988). It follows therefore that the failure to observe any increase in self-directed/displacement behaviour in association with 'Work-Dog' encounters may be attributable to the broad increase in affiliative behaviours. If the use of affiliative behaviours was successful in alleviating the stress response then perhaps no displacement was 'required' or exhibited. It is also possible that because macaques are busy with affiliative behaviours they do not devote any significant increase in time to self-scratching and/or self-grooming behaviour.

2.4.1.4 Maximum number of disturbers

As anticipated, the maximum number of disturbers had a significant effect on macaque coping behaviour. However, this result should be treated with caution as the positive relationship between flight rate and maximum number of disturbers was largely driven by the presence of a single outlier. When this outlier was excluded from analysis the relationship was no longer statistically significant (all other flight rate results remained unchanged). Such an effect would however be unsurprising given that a similar effect has been observed in several other species. For example, the flight initiation distance of Thomson's gazelles (*Eudorcas thomsonii*) decreases when approached by a single hyena (*Crocuta crocuta*) rather than a pack (Walther, 1969), and given the fact that animals may perceive human disturbance as analogous to predation risk (Frid and Dill, 2002) a similar response may be expected in response to potentially threatening encounters with humans. For example, blue tailed skinks (*Emoia impar*) wait longer to flee when approached by only 1 or 2 humans, as compared to 3 (McGowan, Patel, Stroh, and Blumstein, 2014).

2.4.1.5 Position within home range

The relationship between grooming proportion and home range position however is more difficult to explain. No research that I am aware of has investigated this phenomenon (in primates or in any other wildlife) but it raises several possibilities for further research. It may be that because individuals spend proportionally more time in the core of their home ranges than the outer regions that the observed increase is merely an artefact. Indeed, 65% (n=104) of the encounters analysed in this study took place within core home range areas. However it is also possible that macaques feel safer in the core of their home ranges and as such are more willing to engage in vigilance/attention-diverting activities (such as grooming). For example, previous studies suggest that animals are more knowledgeable about refuges and escape routes inside their core home ranges than they are elsewhere (e.g. Eastern chipmunks (*Tamias striatus*) Clarke et al., 1993; Vervet monkeys (*Cercopithecus aethiops*) Isbell et al., 1990), in which case we might expect individuals to feel more secure and thus more likely to engage in grooming behaviour when in more familiar territory.

2.4.2 Potentially rewarding encounters: ‘Recreation’, ‘Recreation-Provisioned’

The behavioural changes observed in association with potentially threatening encounters can be broadly summarised as a response to the threat of predation/harm (extensive escape behaviours) in combination with behaviours (affiliative and to a lesser extent self-directed) that may serve to alleviate the anxiety that these encounters cause. The changes observed in association with potentially rewarding encounters however (specifically encounters in which macaques received human provisioning) may be best understood as components of a strategy that individual macaques adopt to manage intragroup relations in the aftermath of provisioning, rather than as a singular set of responses to an encounter with ‘recreational humans’.

In response to encounters that involved human provisioning, macaques showed changes in all 3 behaviour classes under study. Self-scratching and flight behaviour increased during ‘Recreation-Provisioned’ encounters, as did short affiliative behaviours and number of partners. After provisioned encounters however, approach rate and the number of grooming bouts decreased, whilst the proportion of time spent in the trees increased. Surprisingly no statistically significant changes in coping behaviour were observed in association with ‘Recreation’ encounters. The failure to observe any change is difficult to explain, however it may support the idea that the macaques’ response to ‘recreational humans’ is more strongly linked to the actual receipt of provisioning than to the presence of humans alone. The high value (in energetic terms) of calorie-dense human food and its distribution in time and space (i.e. a clumped, monopolisable resource) greatly increase the potential for intragroup contest competition among provisioned groups (Hsu, Kao, and Agoramoorthy, 2009; Majolo et al., 2013; Van Schaik, 1989). For example, Maréchal (2015) found that Barbary macaques exhibited higher rates of intragroup aggression when tourist groups were closer, as did Tibetan macaques in response to increased provisioning and range-restriction (Berman, Li, Ogawa, Ionica, and Yin, 2007).

2.4.2.1 Escape behaviours

In addition to the increased potential for intragroup aggression associated with human provisioning, animals must also deal with being in close proximity to humans. The increase in flight behaviour observed during provisioned encounters may reflect the anxiety that results as macaques approach, or allow themselves to be approached by humans, in the hope/expectation of receiving provisioning (and then flee as it is received (personal observation)). By maintaining control over their proximity to humans, individuals may better balance the costs (anxiety and the potential for harm) and benefits (food resource) associated with the presence of a donor (Weschler, 1995; Zhao and Deng, 1992). It is surprising therefore that macaques did not flee to the trees or spend a greater proportion of time in the trees during provisioning encounters. Rather, they appeared to remain on the ground during encounters, only spending more time in the trees after encounters had ended. However, Maréchal (2015) observed a similar pattern in response to tourist provisioning encounters. Both male and female macaques were more likely to be on the ground than in the trees, and in open spaces when interacting with tourists. The macaques observed in this study did not ascend to the relative safety of the trees during provisioning encounters either, supporting the assertion by Maréchal (2015) that Barbary macaques may choose to trade-off the potential risks associated with provisioning encounters (e.g. direct human aggression) against the potential rewards (food resources).

The increased proportion of time spent in the trees after provisioning encounters however may be better understood as a strategy employed by individual macaques to monopolise food resources and reduce the risk of intragroup aggression. In order to fully capitalise on human provisioning individuals should presumably consume the resource as quickly as possible and/or without interference from other group members. As such, macaques may spend an increased proportion of time in the trees after provisioning encounters in order to consume valuable food resources without unwanted attention from conspecifics. No studies that I am aware of have examined resource caching and pilfering behaviour in primates, however many corvids cache food for future consumption, a crucial component of which is social context (Emery and Clayton, 2004). That is, many individuals are able to alter their caching (and pilfering) behaviour not only in response to the immediate behaviour of others but also according to whether or not the other individual(s) observed the original caching event (Bugnyar and Heinrich, 2005). Given the similarities between primate and corvid cognition (Emery and Clayton, 2004), an examination of how provisioned macaques respond to and perceive the social context in which they acquire valuable human resources may be a fruitful area for future study. Although macaques have not, to my knowledge, been observed caching food there are clear similarities between the acts of caching and pilfering in corvids, and individual macaques distancing themselves from their group (potentially up a tree as observed in this study) in order to monopolise a valuable resource.

2.4.2.2 Affiliative behaviours

The desire to avoid intragroup aggression may also explain the decrease in approach and grooming behaviour observed after provisioning encounters. If individuals have obtained a valuable food resource and wish to a) consume it alone, and b) avoid aggression from other group members, they should be less likely to approach and/or groom (or tolerate approaches and/or grooming from) other macaques. If macaques perceive group mates as potential competitors during tourist interactions (as suggested by Majolo et al., 2013) then they may distance themselves from other individuals during and/or after these interactions. This idea is supported by the finding of Maréchal (2015) that the likelihood of a macaque having a socially bonded partner within 5 m decreased as the number of tourists present increased. The results of this study lend further support to the idea that macaques may view group mates as potential competitors for human provisioning; in addition to the decrease in approach rate and grooming after provisioning encounters, the rate of short affiliative behaviours (and number of partners) increased significantly during them.

The increased use of short affiliative behaviours (many of which, in certain contexts, are also used as submissive signals, e.g. teeth-chattering and lip-smacking) may help to avert, reconcile, or alleviate the tension generated by competition with group mates over human food. This response is known as the elevator effect (Aureli and De Waal, 1997) and helps to explain how individual primates (including humans) deal with crowding. During brief periods of crowding, individuals habitually modify their behaviour to include more friendly and submissive interactions, and minimise large body movements, eye contact, and loud vocalisations in order to reduce the likelihood or severity of aggression (De Waal, 1989). Indeed, Maréchal (2010) observed an increase in the frequency of short affiliative behaviours when Barbary macaques were in close proximity to tourists (a state in which individuals are generally crowded together in pursuit of clumped resources). Other short affiliative behaviours (such as teeth-chattering) reduce post-conflict anxiety levels among Barbary macaques (McFarland and Majolo, 2011), as does lip-smacking and brief touching among Japanese macaques (Kutsukake and Castles, 2001), all of which were recorded here as short affiliative behaviours. It may be that macaques avoid group mates during (Maréchal, 2015) and after (this study) provisioning encounters in order to avoid intragroup competition, and use more (and more widely spread) short affiliative behaviours to avoid conflict and alleviate the anxiety associated with provisioning encounters.

2.4.2.3 Self-directed behaviours

As observed in numerous primate species (e.g. chimpanzees - Baker and Aureli, 1997; tufted capuchin monkeys (*Cebus paella nigritus*) - Polizzi di Sorrentino et al., 2012); and Barbary macaques (Kaburu et al., 2012)), intragroup conflict can induce anxiety (as measured by an increase in the rate of self-scratching). The increase in self-scratching observed in this study (during provisioned encounters) may be a reflection of and/or an attempt to cope with the anxiety that macaques may experience when competing for human food resources (in close contact) with other group members. Chimpanzees for example, tend to scratch themselves more often when crowded together (Aureli and De Waal, 1997), as do brown capuchins (*Cebus apella*) (Van Wolkenten, Davis, Gong, and de Waal, 2006). Both of these studies also found that the use of submissive signals (many of which are included in the short affiliative behaviours studied here) increased under crowded conditions (as discussed above), suggesting that individuals may adopt an appeasement and inhibition strategy (Aureli and De Waal, 1997) in response to crowded and stressful conditions. Although conflict avoidance in association with provisioned encounters may serve to limit intragroup aggression, it may be that the resulting increase in stress drives the observed increase in self-scratching as an active tension reducing mechanism. For example, an experimental study of female Barbary macaque responses to threat-vocalisations (a stressful event) resulted in an increase in self-scratching behaviour (Gustison et al., 2012).

In order to benefit from human provisioning macaques must also come in to close proximity with humans, which may also induce anxiety. For example, self-scratching rates among provisioned male Barbary macaques increased with the mean number of tourists present (Maréchal et al., 2011), and when the distance between macaques (males and females) and tourist groups decreased (Maréchal, 2015). Similarly, Sulawesi black crested macaque groups have higher self-scratching rates when exposed to tourists than when not (Paulus, 2009). The increase in self-scratching behaviour observed in association with provisioning encounters here, suggests that macaques are willing to incur the psychological and physiological costs associated with increased levels of anxiety (as a result of crowding, competition, and proximity to humans) in order to capitalise on the potential benefits associated with calorie-dense human food.

2.4.2.4 Maximum number of disturbers

The relationship between flight rate and maximum number of disturbers (in association with provisioning encounters) is unsurprising. Flight probability and initiation distance have been positively linked to the group size of disturbers in chamois (*Rupicapra rupicapra*) (Hamr, 1988), several bird species (Burger and Gochfeld, 1988), and although not measuring flight rate *per se*, both black howler monkeys and pygmy marmosets use higher forest strata when exposed to increasing numbers of humans (De la Torre et al., 2000; Treves and Brandon, 2005). In addition, Maréchal (2015) found that Barbary macaques maintained a greater distance from tourists when the number in the nearest group was high. The finding here that flight rates increased with the maximum number of disturbers supports the suggestion that an increase in the number of tourists is perceived as an increased threat.

2.4.2.5 Position within home range

The relationship between grooming proportion and home range position (in relation to potentially rewarding encounters) is however less clear. Many of the same arguments apply to these encounters as apply to potentially threatening encounters (discussed above), particularly the possibility that the increased time spent grooming in core areas is an artefact of the time spent there in general. The 5 study groups had very different degrees of core-home-range-fidelity, i.e. the percentage of the total (95% KDE) home range area occupied by the core (50% KDE) home range area. It is notable that the Blue group's (the most heavily provisioned group) core home range areas only comprised 10% of their total home range area, indicating that they used their core area(s) very heavily in comparison to the rest of their range. Unsurprisingly this core area was focussed around the tourist site where they received regular provisioning. Riley (2008) found a similar pattern among Sulawesi Tonkean macaques (*Macaca tonkeana*); the group occupying the most heavily human-altered habitat utilised a more limited area within their home range, and with greater intensity than the group occupying minimally-altered habitat. With the notable exception of the Yellow group (91%), the other groups' core home range areas comprised approximately 20% of their total home range areas, several of which were also located where macaques could receive provisioning, e.g. lay-bys or small picnic spots within the forest. It is therefore highly probable that the increase in time spent grooming in core home range areas is in fact an artefact of selective home range use rather than a deliberate choice by macaques to increase grooming in the core.

2.4.3 Conclusions

The results of this study highlight the value of considering the effects of multiple types of human/dog encounter on wildlife behaviour and welfare. Although both the potentially threatening and potentially rewarding encounter types appear to induce stress (as indicated by the macaques' increased use of escape, affiliative, and self-directed behaviours), it appears that they do so for different reasons: In the first instance because macaques face the real threat of physical harm from dogs (and possibly humans too); and in the second because they face increased intragroup competition as a result of human provisioning (although the close proximity of human donors no doubt contributes significantly to this). Studies of this kind can further our understanding of how animals respond, not only to encroaching human populations in general, but to the varied type of encounters that result. As the macaque population within Ifrane National Park (and the entire range of the species) comes under increasing pressure from human expansion, it is important for the effective design and implementation of management strategies to consider both the animal welfare issues associated with wildlife tourism and provisioning (Maréchal et al., 2011), and the issues that arise when pastoralists and macaques are forced to share the same, shrinking spaces.

Chapter 3: Expanding human activity and infrastructure in Ifrane National Park, Morocco: spatial and temporal coping strategies of the Barbary macaque

3.1 Introduction

In human-dominated landscapes many wildlife species must deal with human activities and infrastructure within their home ranges. Human activity has the potential to influence animal behaviour in both the short term (as examined in Chapter 2) and the long term. One way in which human activity can cause changes in long-term behaviour is by changing patterns of habitat use. Activities such as hunting, deforestation, and recreation, and infrastructure such as roads and buildings may make habitats more or less available and/or attractive to animals. For example, both grey wolves (*Canis lupus*) and female brown bears show spatio-temporal avoidance of disturbed areas during hours of high human activity (Hebblewhite and Merrill, 2008; Martin et al., 2010). African elephants (*Loxodonta africana*) in human-dominated landscapes use perceived high risk areas (where prior mortality was associated with human occupants) primarily at night, and move through them at greater speed than low risk areas (Graham, Douglas-Hamilton, Adams, and Lee, 2009). And the home ranges of 2 Japanese macaque troops contracted around areas where supplemental feeding by tourists was most intense (a phenomenon that likely contributed to the malnutrition and death of many troop members when that provisioning was abruptly halted during several harsh winters that followed) (Koganezawa and Imaki, 1999).

Understanding the ways in which animals cope with increasingly human-dominated landscapes is an important conservation goal for several reasons. First, any meaningful management efforts require an understanding of how human activity and infrastructure influence animal behaviour (Woodroffe, Thirgood, and Rabinowitz, 2005); this is particularly true when dealing with species of conservation concern such as the Barbary macaque. In common with many endangered primate species (Mace and Balmford, 2000) the declining Barbary macaque population is threatened by extensive habitat loss, degradation, and fragmentation (Ménard et al., 2014b). Despite the creation of multiple national parks within Morocco and a conservation action plan in 2012 (HCEFLCD, 2012), the species receives little practical protection, their habitats are increasingly threatened by human expansion, and their numbers continue to decline (Ménard et al., 2014a). It is therefore essential to understand the consequences of the inevitable and increasing human-macaque overlap, as this is the reality moving forward, either until the creation of an actively protected space for the remaining wild population is accomplished, or in spite of it.

Second, given the importance of dispersal for the maintenance of a genetically viable population (Frankham, Briscoe, and Ballou, 2002), conservation efforts often include the creation of wildlife corridors. Corridors can facilitate the movement of individuals between otherwise isolated habitat fragments, increasing gene flow and reducing inbreeding and genetic drift (Haddad and Tewksbury, 2005). Information about how wildlife habitat use is influenced by human activity and infrastructure is important to the planning of corridors (Bennett, 1999). Indeed, one of the objectives of the Barbary macaque conservation action plan (HCEFLCD, 2012) is the identification of potentially suitable areas for the creation of corridors. This process must take into account not only corridor habitat quality but also how habitat use is influenced by human activity and infrastructure if usable and sustainable corridors are to be created (Harrison, 1992). For example, the corridors that existed in the Bow River Valley of Banff National Park, Alberta, Canada, in the 1980s were so heavily influenced by human activity that the recolonising grey wolf population rarely used them, choosing instead to adopt alternative travel routes (abandoning high quality habitats in the process) (Duke, 1999). Following the recommendation in 1997 that all human structures should be removed and activities reduced within the Cascade corridor, wolf movement through the corridor was restored and regional dispersal facilitated (Duke, Hebblewhite, Paquet, Callaghan, and Percy, 2001).

Third, while an ecosystem can be greatly perturbed by the loss of any species, the loss of those that carry out essential physical ecosystem engineering functions (e.g. seed-dispersal (Corvidae – Pesendorfer, Sillett, Koenig, and Morrison, 2016), soil aeration (*Myospalax fontanierii* – Zhang, Zhang, and Liu, 2003), and dam-building (*Castor Canadensis* – Wright, Jones, and Flecker, 2002)) should be of particular concern to conservation management (Jones, Lawton, and Shachak, 1997). The importance of seed-dispersers to forest ecosystems cannot be overlooked (Gilbert, 1980; Mills, Soulé, and Doak, 1993). The Barbary macaque functions as a seed-disperser (Albert, Savini, and Hunyen, 2013; Herrera, 1995; Ménard, 1984; Ménard and Vallet, 1986), which affects the human population that relies on the forest for consumables and services. In addition to the extraction of wood for burning, construction, and sale, the growth and regeneration of trees (more specifically their roots) stabilises the soil which in turn allows the forest to better retain water (Zuazo and Pleguezuelo, 2009). Given that the fight against desertification is a high priority for the Moroccan government (Ministère de l'Agriculture, du Développement Rural et des Eaux et Forêts, 2001) it is of particular importance to understand how the seed-dispersing macaque population is responding to increasing levels of human activity and infrastructure within the forest.

In terms of habitat use, animals commonly respond to human infrastructure and activity in 2 ways; by altering habitat use to avoid/underuse areas of human infrastructure/habitual activity (spatial avoidance), and/or by using those areas only when human activity is habitually low (temporal avoidance). For example, Eurasian lynx (*Lynx lynx*) in southern Norway establish home ranges that preferentially avoid the most heavily human-disturbed areas (Bouyer et al., 2015), and alter their within-home-range habitat selection to avoid areas with the highest road densities (Basille et al. 2013). African lions (*Panthera leo*) however show no overall spatial avoidance of human-occupied areas (livestock enclosures) in Laikipia County, Kenya, instead using these areas only when human activity is at its lowest (Oriol-Cotterill, Macdonald, Valeix, Ekwanga, and Frank, 2015). A third (and less commonly investigated) response may be to partition behaviour according to both location and time, i.e. areas of human infrastructure/habitual activity are still utilised/avoided, but only at certain times and/or for certain types of behaviour. For example African wild dogs (*Lycaon pictus*) in Botswana select roads when travelling but avoid them when high-speed running or resting (Abrahms et al., 2015).

This suite of potential responses assumes however that areas of human infrastructure and activity are all perceived in a similar way by the animals exposed to them, i.e. as a disturbance to be avoided or managed, when in fact many forms of human influence may be perceived in a positive way; for example (and most notably) areas where the potential to receive or take human food exists. These include refuse sites (Gilchrist and Otali, 2002), tourist sites (Fuentes, Shaw, and Cortes, 2007), and very often roads (Fuentes et al., 2008). It is highly likely that most animals respond to areas of human infrastructure/habitual activity in a multi-dimensional way. They may avoid/underuse certain areas either altogether, at specific times, or when engaged in particular behaviours (or more probably a combination of all 3). And/or they may select/overuse other (or the same) areas when the cost-benefit balance is most strongly in their favour, e.g. at times when such areas are likely to yield the greatest rewards at the lowest potential costs. Such flexibility would allow animals to adapt to local risk/reward conditions by balancing the potential for provisioning (or other high quality resources) against the potential for predation, capture, or other physical harm/negative consequences.

In order to best understand this response it is essential to understand whether animals select particular habitats in association with particular behaviours. Given that different resources are required for the fulfilment of different behaviours it is reasonable to expect that habitat selection differs between activity types; something that should be considered when assessing the influence of human activity and infrastructure on habitat use (Beyer et al., 2010), but that has largely been ignored (Wilson, Gilbert-Norton, and Gese, 2012). Many resource selection studies are based on presence-absence or used-available location data only (often because behavioural data are unavailable, e.g. when data are collected via radio telemetry tracking collars), and these studies are usually still (depending on the aims) useful. However, by considering behaviour-specific habitat selection it may be possible to identify areas that are selected for behaviours that a) have a greater influence on lifetime inclusive fitness, and/or b) are more susceptible to human influence. Understanding the process of habitat selection for different purposes can greatly improve management efforts (Aldridge and Boyce, 2007). For example, because vigilance is reduced when resting and socialising, macaques may refrain from these behaviours in areas that they perceive as potentially risky, e.g. herding routes. However, the same areas may be used for feeding and/or travelling because a) with respect to feeding, the risk may be traded-off against an animal’s energy needs, and b) with respect to travelling, the area may be passed through/by quickly enough that individuals are less susceptible to the risks posed by those areas. Similarly, because macaques may associate roads with the potential for provisioning they may select those areas when feeding and avoid them when engaged in non-feeding behaviours such as socialising, resting, and travelling (in order to maximise the benefits of the time they spend in potentially dangerous (vehicle collisions) areas). Macaques may also alter their habitat selection according to intensity of human use. For example, roads and herding routes that might be avoided when busy could be used for travelling when quiet in order to increase travel speed and efficiency.

This study examines the behaviour-specific habitat use of 5 groups of wild Barbary macaques in INP (measured across multiple seasons) to determine whether human activities and infrastructure within their home ranges influence habitat selection. I test the general hypothesis that macaques will alter their habitat selection in response to human activity and infrastructure. Because the Barbary macaque is a generalist species I predict that their response will be multi-faceted, i.e. spatial, temporal, and behavioural. As observed in Chapter 2 I also expect their response to differ depending on the potential risk or benefit associated with particular types of human activity and infrastructure.

Based on the findings of Chapter 2 (that Barbary macaques appear to perceive encounters that involve/may involve dogs as potentially threatening, and encounters with recreational forest users/tourists as potentially rewarding) I evaluate 2 predictions that test the habitat use strategies discussed above:

Prediction 1: If the possibility of encountering dogs affects Barbary macaque habitat use they will avoid areas where dogs are most frequently encountered, i.e. the herding routes used by shepherds to drive livestock through the study area. Specifically, I test whether:

1a) Macaques avoid herding routes in general (spatial selection).

1b) Macaques select/avoid herding routes in association with habitually low/moderate/high patterns of shepherd/livestock use (spatial and temporal selection).

1c) Macaques select herding routes when feeding and/or travelling, and avoid herding routes when resting and/or socialising (spatial, temporal, and behavioural selection).

Prediction 2: If the possibility of encountering tourists (i.e. those most likely to be sources of provisioning) affects Barbary macaque habitat use they will select areas where tourists are most frequently encountered. Specifically, I test whether:

2a) Macaques select roads in general (spatial selection).

2b) Macaques select/avoid roads in association with habitually low/moderate/high patterns of anthropogenic use (spatial and temporal selection).

2c) Macaques select roads when feeding and avoid them when resting, socialising, and/or travelling (spatial, temporal, and behavioural selection).

3.2 Methods

Data were collected at the same location and on the same study animals described in the previous chapter (see Chapter 2 for full details on the study area and study animals).

3.2.1 Study Design

Resource selection functions (RSFs) were used to examine the relationships between natural and anthropogenic landscape features, and macaque home range use (Figure 17). A RSF is defined as any function that yields values proportional to the probability of use of a resource unit by an organism (Manly, McDonald, Thomas, McDonald, and Erickson, 2002). Logistic regression is commonly used to estimate habitat selection models with used units (e.g. pixels of land in a geographic information system (GIS) model) characterised as 1, and unused (or available) units characterised as 0 (Boyce, Vernier, Nielsen, and Schmiegelow, 2002).

Three general study designs for evaluating resource selection have been established (Thomas and Taylor, 1990). None of these designs are inherently better than the others. They differ only with respect to the level at which resource use and availability are measured; at the population or individual level. Within design 1, all measurements are made at the population level; resource use is measured for the entire study population, and resource availability is measured across the entire study area. Within design 2, individual animals are identified and resource use is measured separately for each; resource availability however is measured at the population level (as in design 1). Within design 3, individuals are identified and both resource use and availability are measured separately for each (Manly et al., 2002).

Because it was possible to obtain behavioural data on multiple known individuals, a modified design 3 approach was adopted and both resource (habitat) use and availability were measured for individual animals (issues of non-independence between individuals within groups were addressed through the use of a complex random effects structure in the final GLMM models). The approach was modified in that habitat use was measured for each individual whilst habitat availability was measured for each study group. Available habitat was defined as the area within a group’s 95% home range, under the assumption that this habitat was equally available to all members of that group.

3.2.2 Data Collection and Processing

A GIS model of the study area was constructed using QGIS 2.14.2-Essen (Open Source Geospatial Foundation, 2016) and all spatial analyses were carried out using tools native to QGIS. Landscape feature values were appended to location records using the QGIS ‘Shapes > Points > Add Polygon Attributes to Points’, and ‘Shapes > Grid > Add Grid Values to Points’ tools in the SAGA (2.1.2) toolbox.

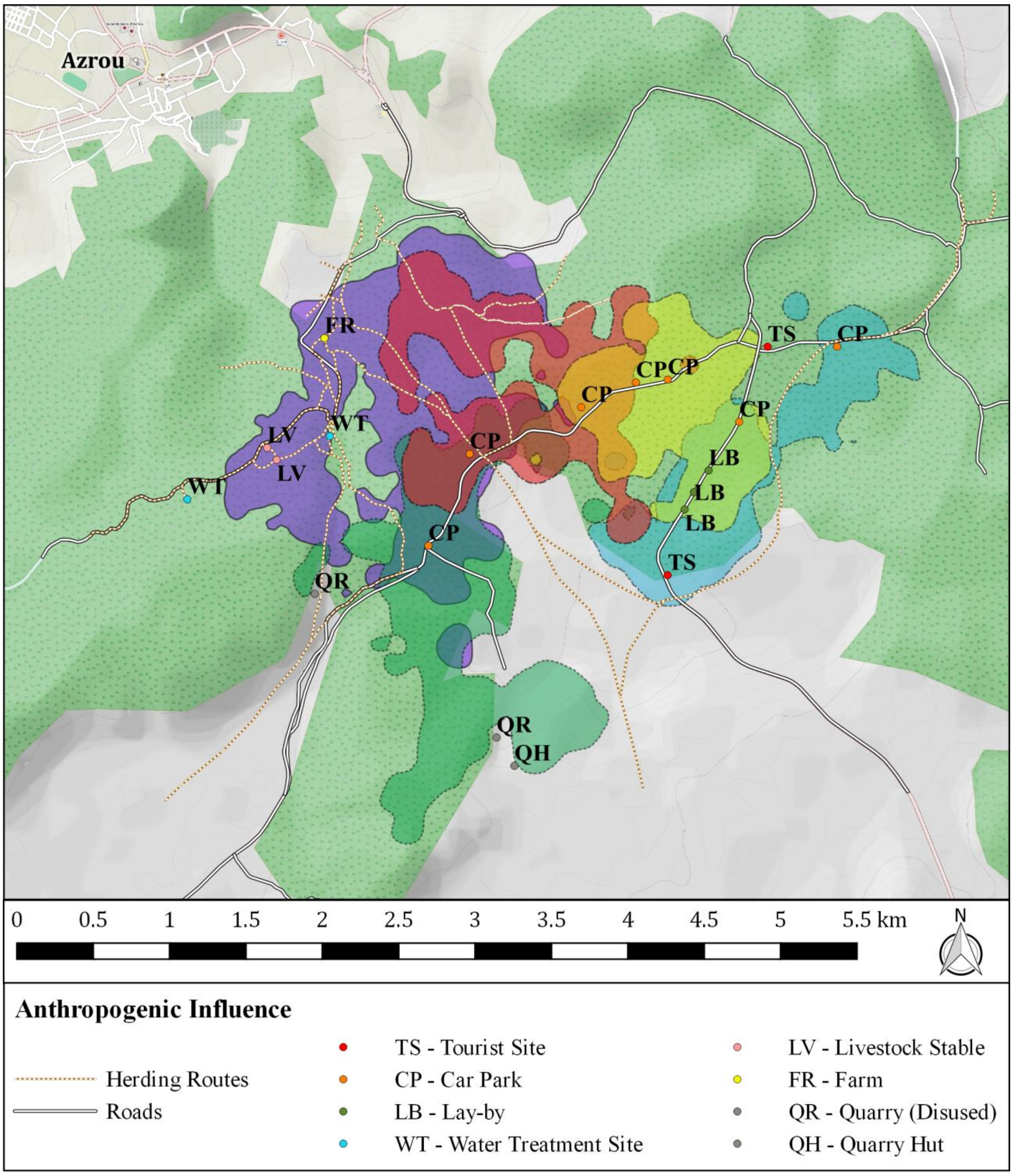

Figure 17. Map of the study area showing macaque home ranges (95% KDE isopleths) and major anthropogenic landscape features. Basemap sources: OpenStreetMap (2016) and Natural Earth data (2016)

3.2.3 Behaviour-specific location data

The study groups were monitored daily between 06:00 and 19:00 (mean daily observation hours ± SE: 9.20±0.19), visibility permitting, from June 2013 to April 2014. To obtain location data, GPS readings were taken every 60 minutes at a point estimated to be the centre of the group (as defined in Chapter 2). All GPS readings were collected using a variety of Garmin handheld GPS devices (all of similar specification to the Garmin etrex Summit HC).

Behavioural data were collected on the hour using instantaneous scan sampling (Altmann, 1974). Scans began 5 minutes before the hour and finished 5 minutes after the hour, or when all group members had been sampled (whichever occurred first), yielding a total of 1998 scan samples and associated GPS locations (Table 9).

Table 9. Scan sampling effort by group.

Group	Data Collection	Total Number of Hourly Scan Samples	Total Number of Behavioural Scan Samples	Mean Number of Behavioural Scan Samples per Individual (±SE)
Blue	May 31, 2013 – April 21, 2014	380	3,439	181±20.2
Green	June 6, 2013 – April 21, 2014	519	4,582	254±33.0
Purple	May 31, 2013 – April 21, 2014	475	3,892	176±26.5
Red	June 8, 2013 - August 15, 2013	233	1,292	184±4.90
Yellow	June 1, 2013 – April 12, 2014	391	1,781	254±46.0

For the purpose of this analysis, behavioural observations were classified into 5 general categories: food-related (hereafter referred to as ‘feeding’), resting, social, travelling, and other (Table 10). Only the first four categories were used in the following analyses.

Table 10. Description of behavioural classes used for analysis.

Behaviour		Definition
Feeding	**Ingesting food**	A monkey is putting food into its mouth. Also chewing food in a feeding bout, i.e. if it does not come from cheek pouches.
	Foraging	A monkey is searching actively for food e.g. scanning the ground for the next thing to eat, or walking around with the head down picking up food items. Includes manipulating food e.g. stripping bark from twigs, cleaning grass roots etc.
Resting	**Resting**	A monkey is stationary and not engaged in any other activity (e.g. not feeding, travelling, or being groomed).
	Resting (huddle)	A monkey is resting as above but huddled with one or more other monkeys of any age class. This option is used almost exclusively when the weather is poor.
	Sleeping	A monkey is resting with eyes closed for a prolonged period of time.
Social	**Allogrooming**	A monkey cleans the surface of another's body (using its fingers or mouth) by licking, nibbling, and picking with the fingers.
	Social (other)	Mating and play behaviour.
Travel	**Travelling**	A monkey is walking, running, or moving (on the ground or through the trees), even if occasionally stopping to look around.
Other		Vigilance, self-grooming, and agonism.

3.2.4 Anthropogenic landscape features

3.2.4.1 Distance from Herding Routes: Continuous variable (0 – 1931 m)

All known herding routes were mapped on the ground by walking their length with a handheld GPS unit (Garmin etrex Summit HC) set to record a position fix every 10 m. The resulting tracks were digitised, merged, and incorporated as a vector layer within the GIS model of the study area. This vector was rasterised using the QGIS 'Shapes > Grid > Gridding > Shapes to Grid' tool in the SAGA (2.1.2) toolbox, and 'distance from' raster maps were created using the QGIS 'Raster > Analysis > Proximity (Raster Distance)' tool.

3.4.2.2 Distance from Roads: Continuous variable (0 – 2014 m)

Road data derived from OpenStreetMap.org were obtained from MapCruzin.com (http://www.mapcruzin.com/free-morocco-arcgis-maps-shapefiles.htm) and incorporated as a vector layer within the GIS model of the study area. This vector was rasterised using the QGIS 'Shapes > Grid > Gridding > Shapes to Grid' tool in the SAGA (2.1.2) toolbox, and 'distance from' raster maps were created using the QGIS 'Raster > Analysis > Proximity (Raster Distance)' tool.

3.4.2.3 Intensity of Use (Herding Routes and Roads): Categorical variable (3 levels: Low, Moderate, and High)

Intensity of use variables were derived from data gathered during regular transect surveys of the study area (Ganzhorn, Rakotondranary, and Ratovonamana, 2003). Fifteen transects were established at the start of the study (Figure 18) but as the data required to estimate home ranges accumulated it became clear that 2 transects (the 2 most westerly transects in Figure 18) did not intersect any of the study groups' home ranges and these were dropped from sampling. Transect coverage per km^2 home range was as follows: Blue (0.78 km); Green (0.89 km); Purple (0.93 km); Red (0.73 km); Yellow (0.79 km). Transects were 900 m long (straight-line distance, not over-land) and were placed according to a stratified random sampling design, i.e. the start point of the initial transect was randomly determined but the subsequent spacing and orientation of transects was determined using the software Distance 6.0 release 2 (Thomas et al., 2010). A stratified random sampling design maximises coverage and data collection effort, allowing transects to be placed perpendicular to salient environmental features (in this case the road bisecting the study area), avoiding an unrepresentative sampling gradient along the length of the feature (Figure 18).

All transects were walked at different times of day, in different directions, once every 2 weeks and all sightings of humans, livestock, dogs, and motor vehicles were recorded (detailing the type and number observed). Each transect was walked 24 times in total (with 3 exceptions that were walked 23 times), for a total length of 21.6 km per transect (and 20.7 km respectively). The total transect distance walked was 2222.1 km and the total transect observation time was 312 hours and 9 minutes. Where transects crossed a road, observers paused for a period of exactly 5 minutes and recorded the number and size (small, medium, large; e.g. motorbike, four-door family car, logging truck, respectively) of vehicles that passed. Three hundred and seven road counts were conducted for a total observation time of 25 hours and 35 minutes.

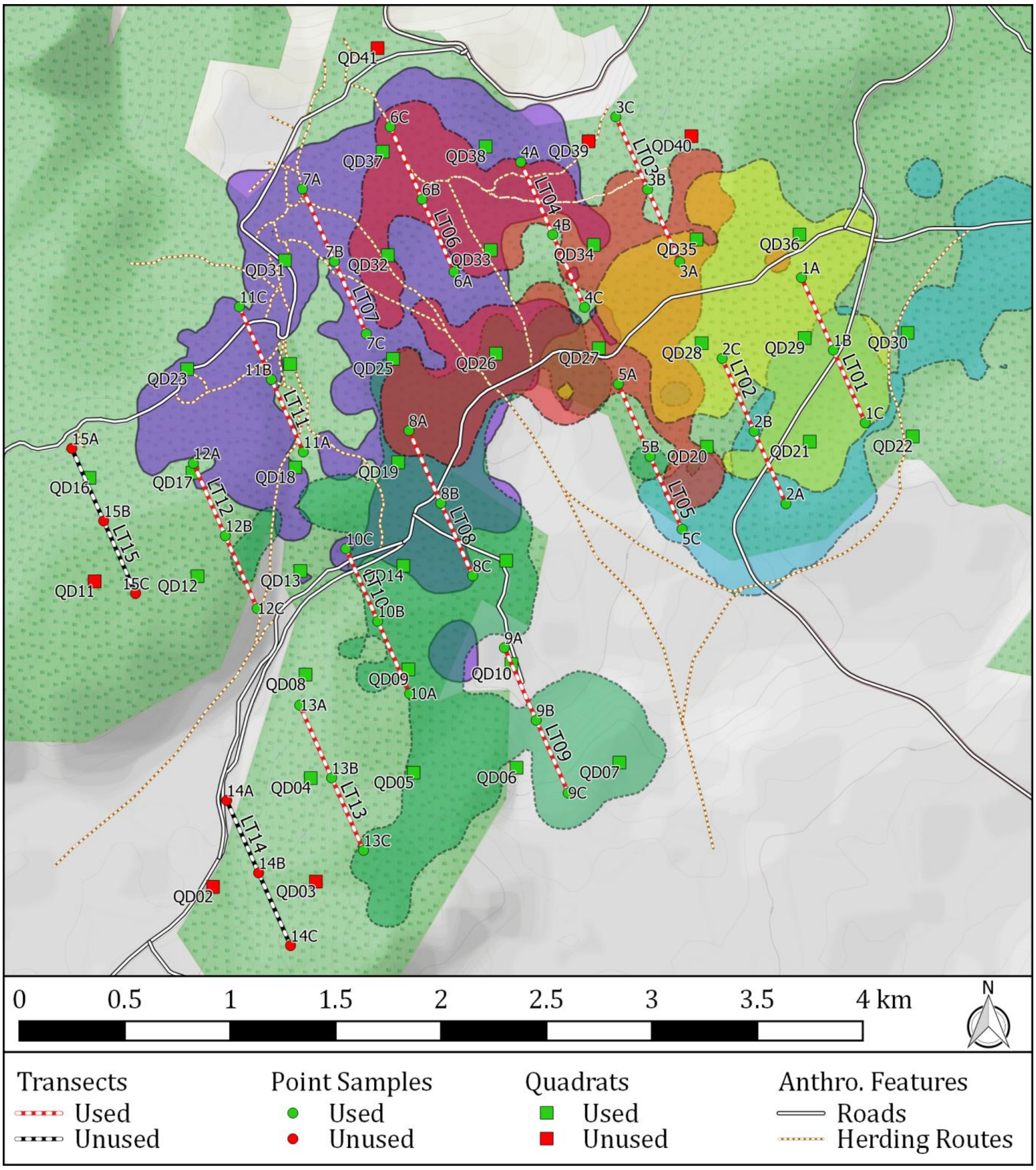

Figure 18. Map of the study area showing placement of transects, point samples, quadrats, roads, and herding routes. Basemap sources: OpenStreetMap (2016) and Natural Earth data (2016)

Herding route and road use varied throughout the day as shown in Figures 19 and 20. Each hour of the day was assigned a low/moderate/high value (for herding routes and roads separately) according to whether it fell below, within, or above the 95% confidence interval of the mean.

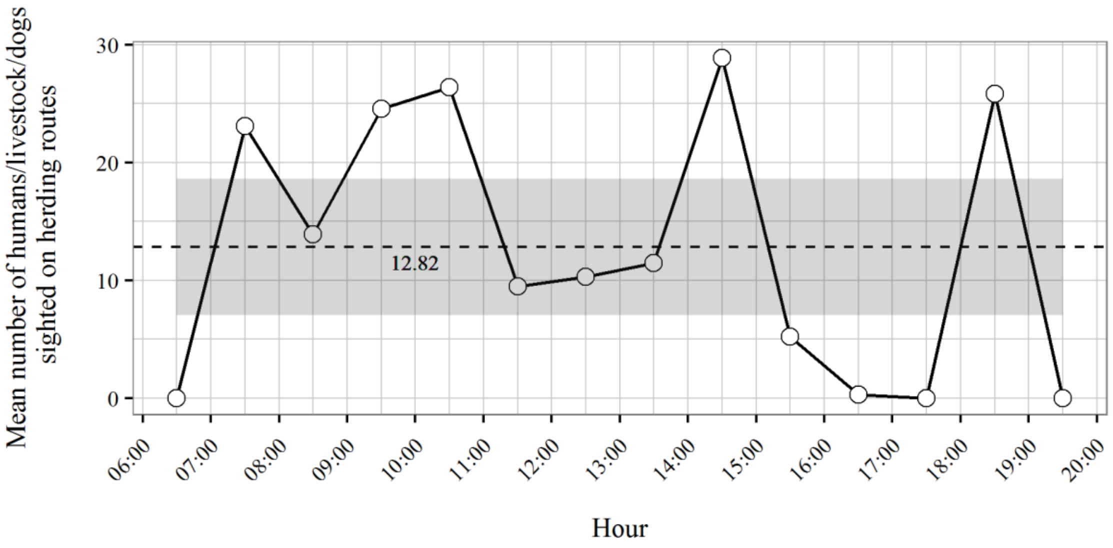

Figure 19. Herding route intensity of use. Dashed line represents mean values (presented underneath lines) and shaded area represents the 95% confidence interval around the mean.

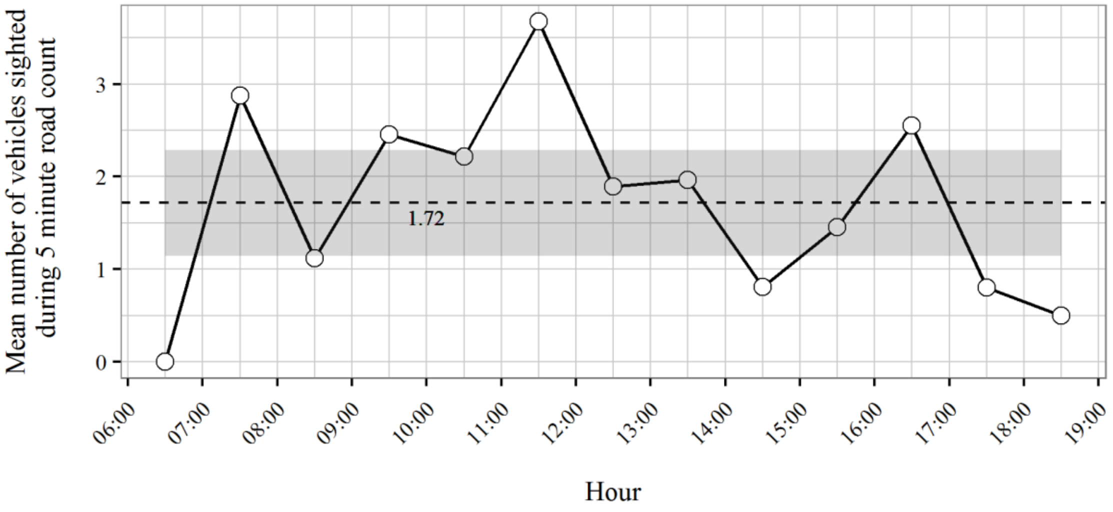

Figure 20. Road intensity of use. Dashed line represents mean values (presented underneath lines) and shaded area represents the 95% confidence interval around the mean.

3.4.2.4 Feature Density (Herding Routes and Roads): Continuous variable (0 – 2.944 and 0.764 – 1.243, respectively).

The length (km) of herding routes and roads per km^2 within each group's home range were added to the RSF models as control variables to account for (1) the different levels of 'exposure' experienced by each group, and (2) the amount of 'undisturbed' space left available to each group.

3.2.5 Natural landscape features

3.2.5.1 Cover: Categorical variable (3 levels: Dense, Moderate, and Open)

Cover type was estimated from a digitised satellite map of the study area and ground-truthed (i.e. the coverage and extent indicated by the satellite image was checked for accuracy at multiple points on the ground by observers) using (1) vegetation density data gathered during scan samples (detailed below), (2) canopy cover data gathered during disturbance point sampling (detailed below), and (3) regular mapping data collected during the course of the study that was used to build the GIS model of the area. Three general cover classes were established: dense forest (50% to 100% tree cover), moderate cover (1% to 49% tree cover), and open (no tree cover).

3.2.5.2 Productivity: Continuous variable (0-100)

Productivity was estimated from the proportion of time individuals spent feeding during 556 hours of focal animal sampling (Altmann, 1974). These data were ground-truthed using (1) percentage cover data (e.g. grass, herbs, bare earth etc.) gathered during quadrat sampling of the study area (detailed below), (2) undergrowth quality and abundance data gathered during point sampling of the study area (detailed below), and (3) tree productivity data (e.g. fruits, lichen, and other edible structures) gathered during point sampling of the study area (detailed below).

Quadrat sampling

Forty 2 m x 1 m quadrat sampling plots (Ganzhorn et al., 2003) were established at the start of the study (Figure 18) but as the data required to estimate home ranges accumulated it became clear that 7 plots did not fall within any of the study groups' home ranges and these were dropped from sampling. Vegetation sampling was conducted once every 2 weeks to assess the abundance and seasonal availability of potential macaque food items on the ground. Thirty-three quadrat plots were sampled an average of 11.6 times (range 10 -13) over the course of the study. A visual estimate of the percentage of the quadrat area covered by herbs, grass, rock, etc. was recorded at each sampling. These percentage cover data were used to compare the availability of edible items between quadrats.

Quadrats were placed (Figure 18) according to the same stratified random sampling design principles as described for the transect placement above. A GIS shapefile of the study area and the number of quadrat locations to be created were input to the Distance 6.0 release 2 software (Thomas et al., 2010) and the most efficient quadrat placement (in terms of sample effort and coverage) was output as a set of coordinates.

Point sampling

Forty-five point sampling locations (5 m radius) (Ganzhorn et al., 2003) were established in conjunction with the transect samples detailed above. Three points were associated with each transect, 1 at the start, middle, and end of each line (Figure 18). Because 2 transects were dropped from sampling this meant the loss of 6 point samples as well, leaving a total of 39 regularly sampled points. These were sampled on the same schedule as the transects and yielded the same number of samples (per point) as the associated transects. Undergrowth quality and abundance at each point was assessed using the following scale, adapted from Camperio-Ciani, Martinoli, Capiluppi, Arahou, and Mouna (2001):

0 = No grass, shrubs or plants; bare earth and/or livestock debris

1 = 1 - 25% of the radius is covered with grass and/or shrubs

2 = 26 - 50% of the radius is covered with grass and/or shrubs

3 = 51 - 75% of the radius is covered with grass and/or shrubs

4 = 76 - 100% of the radius is covered with grass and/or shrubs

A raster map of productivity values was generated using the QGIS ‘Raster > Interpolation’ tool, with proportion of time spent feeding as the triangulated irregular network (TIN) interpolation attribute, and a cell size of 30 m^2. Spatial interpolation is the process of using points with known values to estimate values at other unknown points. A common TIN algorithm is called Delaunay triangulation; it creates a surface formed by triangles based on nearest neighbour point information. Circumcircles are generated around selected sample points and their intersections are connected to a network of non-overlapping triangles, the end result of which is a continuous raster surface. The resulting raster values were normalised to a range of 0-100 to allow meaningful comparison between areas. High values correspond to areas of high productivity and low values correspond to areas of low productivity.

3.2.5.3 Home Range Overlap: Binary variable (2 levels); (1 = area contained within more than 1 group's home range; 0 = area contained within 1 group's home range only).

Overlap was determined by merging the home range shape files of each group and classifying any area utilised by more than 1 group as 1, and any area used only by 1 group as 0.

3.2.5.4 Slope: Continuous variable (0 – 44.7915)

Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) Global Digital Elevation Model (GDEM) data were obtained from the USGS Earth Data website (U.S. Geological Survey, 2015) and incorporated as a 1 arc-second (approximately 30 m^2) elevation grid, from which slope data were derived using the QGIS 'Raster > Terrain Analysis > Slope' tool. High slope values correspond to steep gradients, low values correspond to shallow gradients, and zero values represent primarily flat terrain.

3.2.6 Additional analyses

3.2.6.1 Relationship between areas of home range overlap and productivity

Because the model results (see section 3.3.1 Feeding behaviour) indicated that macaques strongly selected areas of home range overlap for feeding, a Welch 2 sample t-test was carried out to determine if mean productivity values differed between areas of home range overlap and areas of exclusive use. This test was carried out to ascertain whether macaques selected areas of home range overlap when feeding because these areas were, on average, more productive

3.3.6.2 Relationship between group sighting order and road proximity

Because the model results (see sections 3.3.1 through 3.3.4 (All behaviours)) indicated that macaques strongly selected areas close to roads, a Wilcoxon rank sum test was carried out to determine if the first hourly GPS positions of a group (per day) were, on average, closer to roads than other hourly GPS positions throughout the day. This test was carried out to ascertain whether the fact that researchers accessed the study site by road (and so necessarily began searching for groups from the road) may have had an effect on the 'distance from road' component of the resource selection models.

3.2.7 Modelling procedure

Behaviour-specific GPS locations were imported into QGIS and 10 random locations were generated (within the appropriate home range) per observed location. Observed and random locations were restricted to within 95% KDE group home ranges because the majority of macaque activity is restricted to these areas and it is difficult to objectively define an ‘available’ area outside a group’s home range (Wilson et al., 2012).

Logistic regression was used to estimate RSFs by the comparing landscape characteristics (as detailed above) of used locations to those of available locations for each individual, within their home range; specifically, how those landscape characteristics related to the relative probability of use and the relative probability of a behaviour occurring. Four generalised linear mixed models (GLMMs) with binary response variables (1 = used, 0 = available), binomial error distributions, and logistic links were used to compare habitat selection by behaviour type. Random intercepts for subject (nested within scan, within group) were included to account for correlation of habitat use within individuals, between individuals within a group, and between individuals within each hourly scan. Scan was included as a random intercept term to account for the fact that in order to maintain contact with the group at large, individuals may not be entirely free to choose their activity independent of the rest of their group members. For example, if the group at large is travelling, although an individual is technically free to feed, rest, or socialise, they risk losing the group if they fail to travel in unison. As such, behaviours within scans may be correlated in a way that behaviours between scans are not. All RSF models were fitted using the ‘glmer’ command of the ‘lme4’ package (Bates, 2010) within the R platform (Version 3.2.3) (R core Team 2015) and estimated using Laplace approximation as recommended by Bolker et al. (2009).

Models were checked for evidence of collinearity between predictors using variance inflation factors (‘vif’ function in the package ‘car’ (Fox and Weisberg, 2011)) as recommended by Barr et al. (2013). Because logistic regression is particularly sensitive to collinearity among explanatory variables, 2 distance-based variables were dropped from the models; ‘distance from work structures’ and ‘distance from provisioning sites’. ‘Distance from work structures’ was highly correlated with ‘distance from herding routes’ as (due to their function as farms, stables etc.) all of these structures were located along or at either end of herding routes. A similar situation was observed with ‘distance from provisioning sites’ and ‘distance from roads’ as all provisioning sites were either lay-bys, car parks, or recreational areas directly accessible by road. ‘Distance from herding routes’ and ‘distance from roads’ were retained because I anticipated that their linear nature would exert a greater influence on macaque habitat use than the point features associated with work structures and provisioning sites. In order to allow for a meaningful comparison between behaviour types all distance-based variables were centred and standardised by subtracting the variable’s mean from each score and dividing the result by the variable’s standard deviation.

In order to avoid the problems associated with stepwise model selection (Whittingham et al., 2006) the significance of all fixed effects was tested using full models. The use of identical models for each dependent variable also allowed for a simple comparison of behavioural responses. The significance of each full final RSF model was assessed by comparison to a corresponding null model (i.e. an intercept-only model with no independent variables) using a likelihood ratio test (‘anova’ function in the ‘stats’ package (R Core Team 2015) with test set to “Chisq”) (Zuur et al., 2009). The significance of the individual fixed effects (independent variables) of significant models was determined based on the Wald *z*-statistics and *p*-values provided by ‘glmer’. All statistical tests were two-tailed with α set to 0.05.

Model validation was carried out using *k*-fold cross-validation, testing predictive performance using area under the curve (AUC) (Boyce et al., 2002). This procedure partitions the original data set into *k* bins and performs *k* iterations of training and validation in which a different bin is held out each time for validation whilst the remaining *k*-1 bins are used to train the model. As recommended by Boyce et al. (2002) 10 folds were used ($k = 10$) to evaluate the predictive performance of the RSF models. The AUC of a receiver operating characteristic (ROC) curve represents the relative proportions of correctly and incorrectly classified predictions over a range of threshold levels by plotting true positives versus false positives for a binary classifier system. As defined by Swets (1988) models can be classed as: 1) non-informative (AUC=0.5); 2) less accurate ($0.5<\text{AUC}\leq0.7$); 3) moderately accurate ($0.7<\text{AUC}\leq0.9$); 4) highly accurate ($0.9<\text{AUC}<1$); and 5) perfect (AUC=1).

3.3 Results

Of the 10362 macaque locations used in this analysis, 4623 (44.61%) were classified as feeding, 1586 (15.31%) as resting, 2532 (24.44%) as social, and 1621 (15.64%) as travelling. An average of 142 (SE=10) observations were obtained from each individual, and 2072 (SE=446) from each group. The spatial and temporal relationship between used macaque locations and 6 landscape features/characteristics (herding routes, roads, forest cover, productivity, home range overlap, and slope) were used to create 4 separate resource selection function models; one for each behaviour studied. The results of these models relate the relative probability of an area being used for a particular behaviour to the landscape characteristics present there (for full model results see Appendix B - Tables 1 and 2). Model results varied substantially between behaviours with respect to the significance and direction of parameter estimates, and with respect to predictive performance (AUC of ROC as detailed above) (Table 11).

Table 11. Model significance (Chi-Square test) and validation (AUC of ROC curve) of behaviour-specific resource selection function models for the 4 behavioural activities considered in this study. Statistically significant ($\alpha=0.05$) *p*-values are underlined and in bold type.

Test	**Model**			
Null vs. full model: Chi-Square Test	**Feed**	**Rest**	**Social**	**Travel**
N	49841	17344	27653	18146
df	17	17	17	17
χ^2	189.51	185.51	286.24	105.76
***p*-value**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Model validation: AUC of ROC curve	0.91	0.89	0.87	0.82

3.3.1 Feeding behaviour

Macaques avoided open areas when feeding, instead selecting areas of high productivity, and areas where their home ranges overlapped with those of neighbouring groups. They avoided areas close to herding routes, and the relative distance from these routes increased further during periods of habitually moderate and high herding route activity. Macaques showed no general preference for areas close to roads whilst feeding, however individuals were generally found closer to roads than would be expected by chance during periods of habitually moderate and high road activity (Figure 21; Appendix B – Table 1).

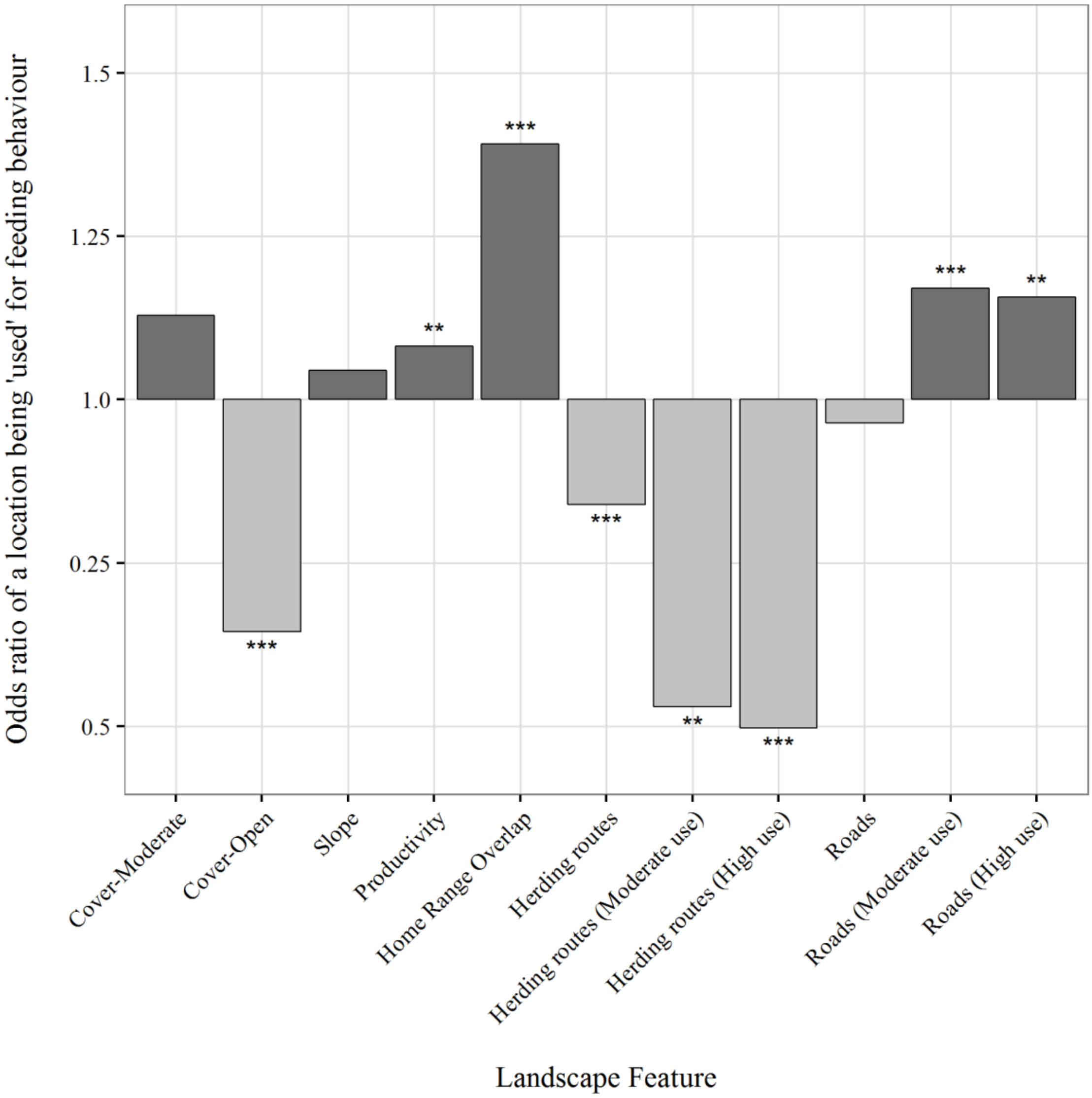

Figure 21. Odds ratio of a location being 'used' for feeding behaviour in relation to landscape features. Odds greater than 1 indicate a higher than even likelihood of selection and odds less than 1 indicate a lower than even likelihood of selection. Asterisks indicate statistically significant deviation from the even likelihood, in the form of either selection (value >1) or avoidance (value <1). * P<0.05; **P<0.01; ***P<0.001.

3.3.2 Resting Behaviour

Macaques avoided open areas when resting and selected areas where their home ranges overlapped with those of neighbouring groups. They avoided areas close to herding routes, but no statistically significant change in proximity was observed in association with either moderate or high periods of habitual herding route activity. They did however select areas close to roads when resting, a tendency that also remained unchanged in association with habitually moderate or high periods of road activity (Figure 22; Appendix B – Table 1).

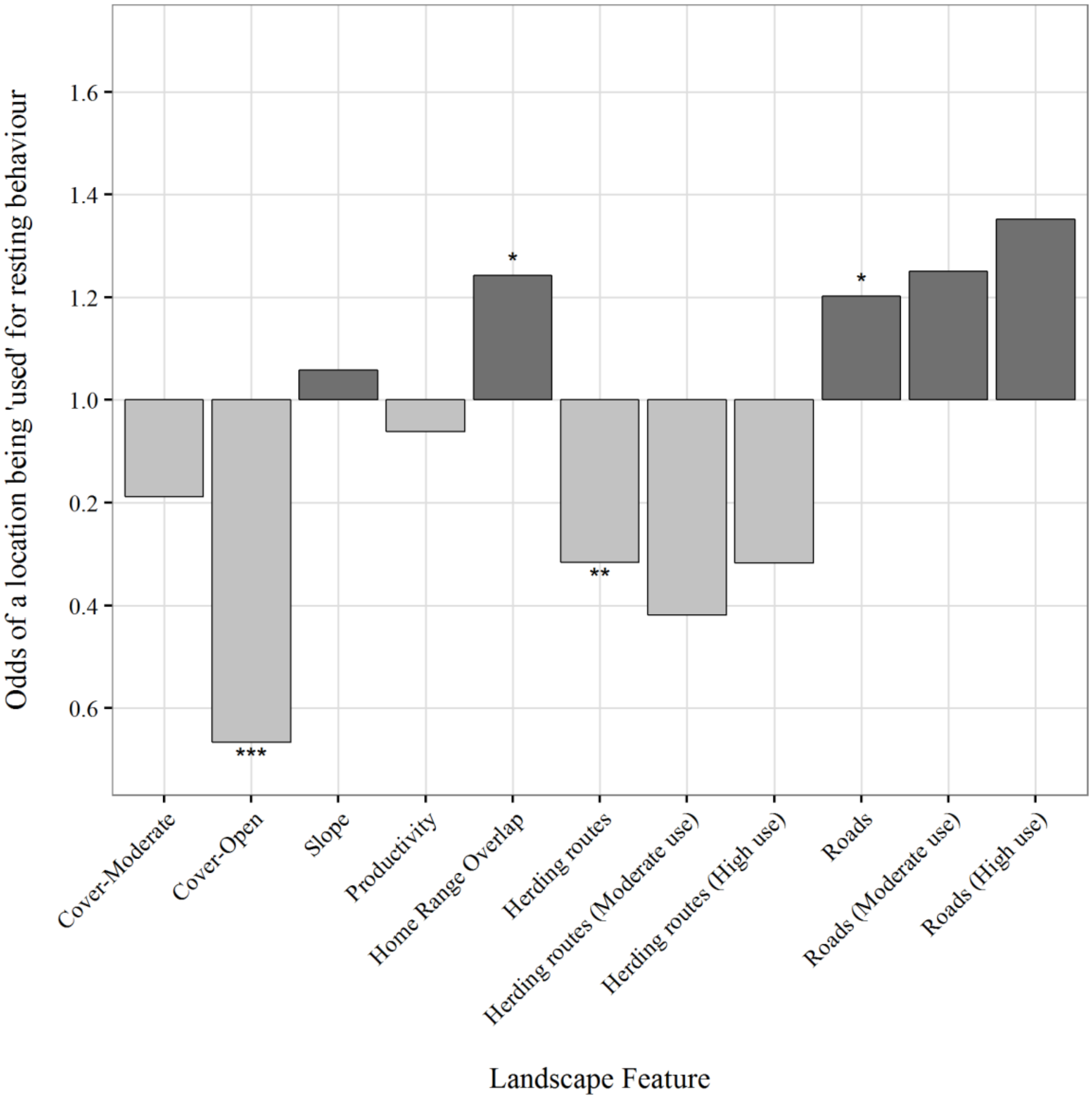

Figure 22. Odds ratio of a location being ‘used’ for resting behaviour in relation to landscape features. Odds greater than 1 indicate a higher than even likelihood of selection and odds less than 1 indicate a lower than even likelihood of selection. Asterisks indicate statistically significant deviation from the even likelihood, in the form of either selection (value >1) or avoidance (value <1). * P<0.05; **P<0.01; ***P<0.001.

3.3.3 Social Behaviour

Macaques avoided open areas and areas of high productivity during social behaviour. They also avoided areas close to herding routes, but no statistically significant change in proximity was observed in association with either moderate or high periods of habitual herding route activity. Conversely, macaques selected areas close to roads during social behaviour, a tendency that remained unchanged in association with habitual periods of either moderate or high road activity (Figure 23; Appendix B – Table 2).

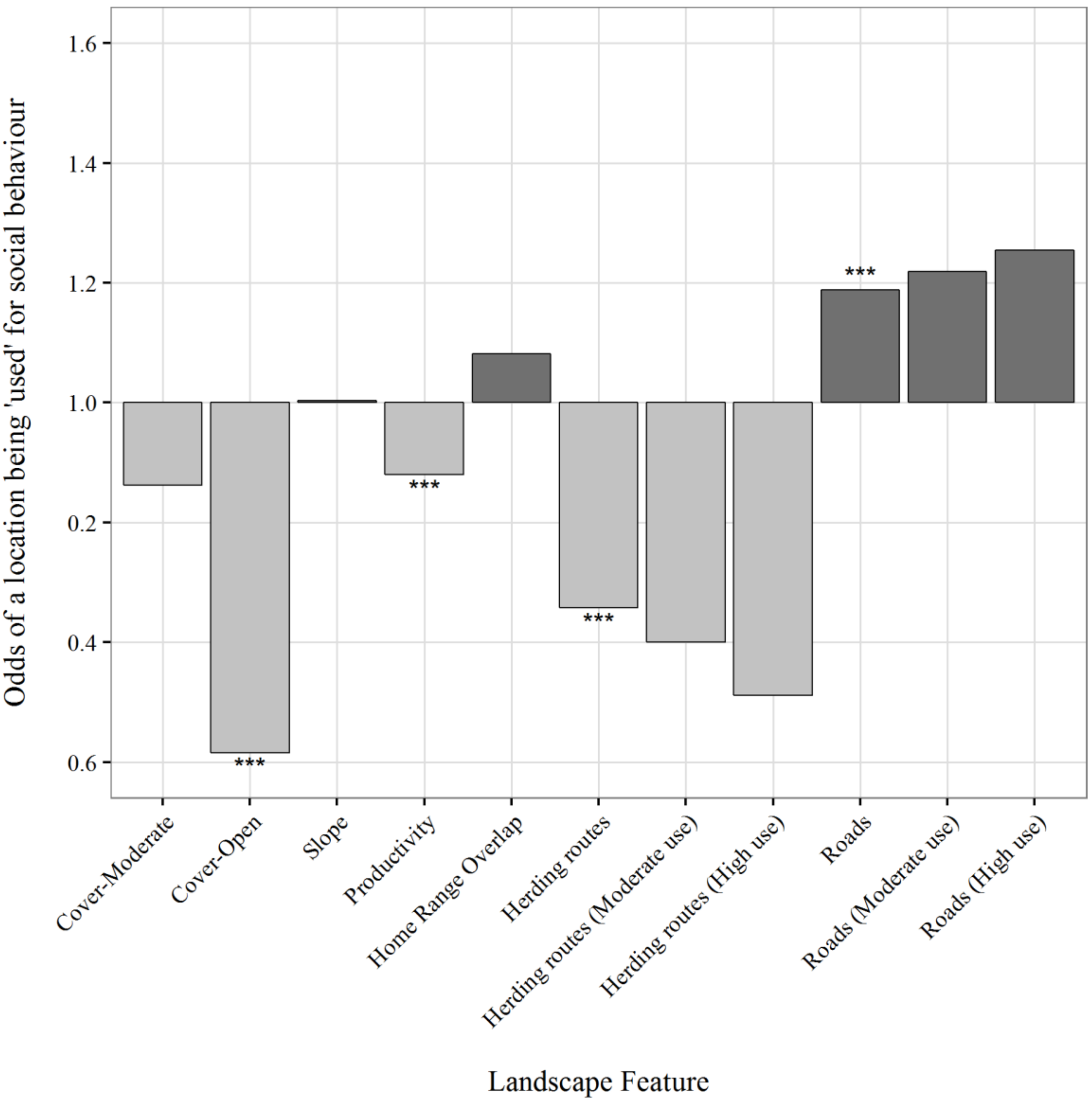

Figure 23. Odds ratio of a location being 'used' for social behaviour in relation to landscape features. Odds greater than 1 indicate a higher than even likelihood of selection and odds less than 1 indicate a lower than even likelihood of selection. Asterisks indicate statistically significant deviation from the even likelihood, in the form of either selection (value >1) or avoidance (value <1). * P<0.05; **P<0.01; ***P<0.001.

3.3.4 Travel Behaviour

Macaques avoided open areas when travelling and areas close to herding routes, but only during periods of habitually moderate and high activity. Macaques showed no general preference for/avoidance of areas close to roads whilst travelling, and no statistically significant change in road proximity was observed in association with either moderate or high periods of habitual road activity. They did however select steep slopes when travelling (Figure 24; Appendix B – Table 2).

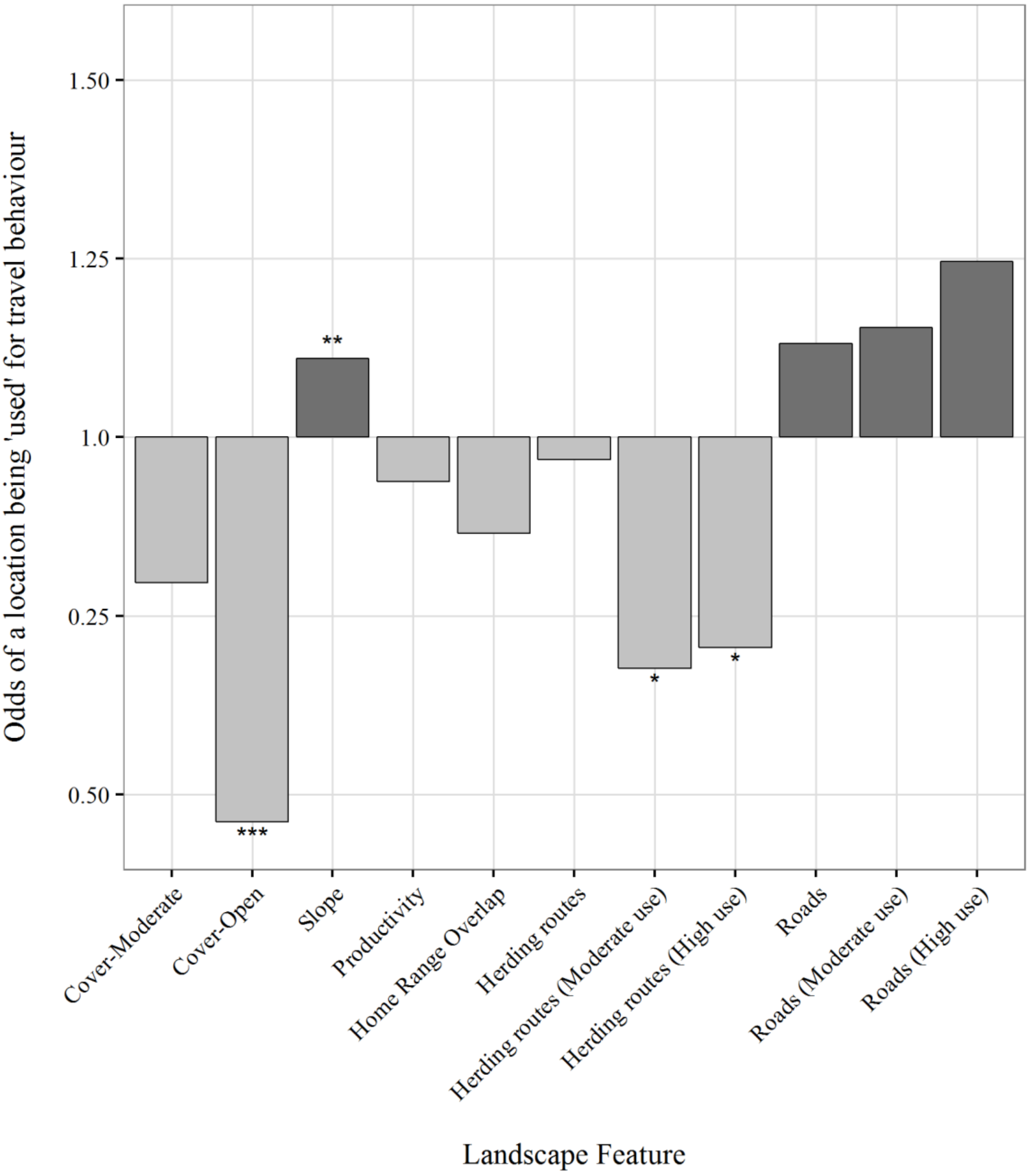

Figure 24. Odds ratio of a location being 'used' for travel behaviour in relation to landscape features. Odds greater than 1 indicate a higher than even likelihood of selection and odds less than 1 indicate a lower than even likelihood of selection. Asterisks indicate statistically significant deviation from the even likelihood, in the form of either selection (value >1) or avoidance (value <1). * P<0.05; **P<0.01; ***P<0.001.

3.3.5 Relationship between areas of home range overlap and productivity

Areas of home range overlap were on average more productive than areas used by a single group only. There was a significant difference in the mean productivity values for areas of home range overlap (M=38.65, SD=19.87) and areas used by a single group only (M=37.07, SD=21.28), t(7192)=3.7, p=<0.001.

3.3.6 Relationship between group sighting order and road proximity

There was no significant difference in the mean ranks of 'distance from road' values for first hourly GPS positions of the day (Mdn=207.36 m) and all subsequent hourly GPS positions (Mdn=183.71 m), *W*=199810, p=0.228.

3.4 Discussion

As predicted, Barbary macaques showed evidence of selective habitat use in association with human activity and infrastructure on spatial, temporal, and behavioural scales. Three broadly consistent patterns of selection/avoidance were observed: macaques exhibited a general spatial preference for areas close to roads and a general spatial avoidance of both open areas (i.e. with no tree cover) and areas close to herding routes. Selection and/or avoidance of all other landscape features varied according to behaviour type, highlighting the importance of considering how space is used when conducting resource selection studies, in addition to whether it is used.

3.4.1 General habitat selection

Macaques consistently avoided both open areas and as predicted (prediction 1a), areas close to herding routes. The only exception to this pattern was observed when macaques were travelling; during travel behaviour herding routes were not avoided generally, rather only when habitual herding route activity was classed as ‘moderate’ or ‘high’ (in fulfilment of predictions 1b and 1c). The avoidance of both open areas and areas close to herding routes is likely a response to a) the increased probability of encountering predators (particularly dogs) in these areas, b) the lack of cover in these areas, and c) the diminished possibilities for escape if predators are encountered. As indicated by the results of Chapter 2, flight (specifically tree ascension) is an important part of the macaque response to dog encounters, and in open, unforested habitat this response is rendered unfeasible. Similarly, many of the herding routes that traverse the study area are on open ground (Figure 17), and those that are not are largely broad and treeless. Given the diminished capacity for escape in treeless areas, coupled with the high probability of encountering dogs on the herding routes (compared to elsewhere within the study area (with the exception of the 2 main tourist sites)) it seems reasonable to infer that the macaques monitored in this study avoid both open areas and herding routes primarily to avoid potentially dangerous dog encounters. This is supported by the observations of Ciani et al. (2005), Ménard (2002), and Mehlman (1984) that macaque density is consistently lowest in open grassland areas; that they are largely unwilling to leave forest cover for the open; and that dogs can alter macaque ranging patterns by creating ‘avoidance routes’ that macaques follow.

Areas close to roads however were (with the exception of travel behaviour) generally selected for (in support of prediction 2a). Macaques showed no general preference for areas close to roads when feeding, rather preferring those areas only when traffic activity was habitually ‘moderate’ and/or ‘high’ (in support of predictions 2b and 2c). This suggests that macaques may perceive the roads that pass through their home ranges as either relatively benign (certainly in comparison to herding routes) or potentially rewarding features. Indeed, 38% of the human-macaque provisioning encounters utilised in this analysis (n=22) occurred within 20 m of a road. It is possible that the observed preference for areas close to roads is in some part attributable to the fact that researchers accessed the study site by road (and so necessarily began searching for groups from the road), however there was no significant difference in road proximity between the first sightings of a group (per day) and subsequent sightings. As such it seems more likely that the macaques associate some positive experience with these areas. Despite the seemingly obvious danger of being struck and injured/killed by road traffic (6 macaques (all from the Blue group) died as a result of vehicle collisions between April 2013 and January 2015), 2 of the study groups (Blue and Yellow) spent a great deal of time near to and on roads. It may be that the macaques are either unaware of the danger, or much more likely, willing to tolerate it in order to gain access to calorie-dense human food. In addition to the energetic benefits of consuming food in excess of metabolic needs (i.e. to buffer against the possibility of future food shortage) macaques may also be conditioned to seek out specific gustatory rewards (such as sweetness) found only in human food (Fa, 1988); the pursuit of which may also influence the perceived cost/benefit balance. Although the potential cost of roadside provisioning is extremely high (serious injury and/or death) it may be perceived by the macaques as, in comparison to the potential reward (the rapid fulfilment of one’s daily energy requirement), an infrequent and possibly acceptable price to pay. For every recorded instance (across the entire study data set) of human roadside provisioning (n=60), 0.1 macaques were harmed as a result of vehicle collisions. However this figure may be artificially high given that there were no doubt many more unrecorded provisioning encounters than road deaths.

Similar trade-offs have been observed in numerous other studies of primate behaviour in relation to roads, including in other members of the genus *Macaca*. Despite the road-accident deaths of 35 long-tailed macaques (*Macaca fascicularis*) in 1 year (2.4% of the population), the population that inhabits the Bukit Timah nature reserve in Singapore habitually waits at roadsides for human food, and both the number and group size of macaques increases with increased proximity to roads and human settlements (Mun, 2014). A similar effect on group size was observed among 5 rhesus macaque groups in the Madhya Pradesh tiger reserve in India (Pragatheesh, 2011). Group size was positively related to the number of people feeding monkeys by the road, even though the highest concentrations of road-kills were clustered around the roadside areas where feeding most frequently occurred (usually by throwing food into the middle of the road (as also observed in this study)). Fifty-four road-deaths were recorded over the 11 month study period, a figure that represents 17.7% of the study population, although this percentage is probably an overestimate given that several other macaque groups occupied the study area and likely contributed to the road-death count.

It is notable that whilst feeding, macaques showed a specific preference for areas close to roads when road activity was at moderate and high levels, whereas when resting and socialising, macaques showed only a general preference for areas close to roads. It may be that macaques preferentially rest and socialise in areas close to roads in the aftermath (or in anticipation) of roadside provisioning; only moving closer when traffic activity is habitually moderate or high in order to maximise the chances of receiving human food. This indicates an awareness of the risks and benefits associated not only with road proximity but also with the level of road traffic. Chimpanzees (*Pan troglodytes*) at Bossou in Guinea wait longer to cross wide roads than narrow ones and also wait longer on wide roads as traffic volume increases (Hockings, Anderson, and Matsuzawa, 2006). This suggests that chimpanzees are aware of and adapt to variations in perceived risk associated with roads. The macaques in this study appear able to do the same whilst also balancing this risk against the potential rewards. When roads are busy the potential provisioning rewards may outweigh the perceived risks. When roads are not especially busy however the potential rewards may be low enough that the risk (even a reduced risk) is no longer worth the reward, and as such macaques withdraw to rest or socialise nearby instead.

3.4.2 Behaviour-specific habitat selection

3.4.2.1 Feeding behaviour

In addition to a preference for roads when traffic activity was habitually moderate and/or high (discussed above) macaques also preferred areas of high productivity and home range overlap when feeding. The preference for areas of high productivity is selfexplanatory, however the preference for areas that overlapped the home ranges of neighbouring groups is not. It seems unlikely that macaques purposely choose overlapping areas in which to feed but rather that they choose the most productive areas available to them. If any of these areas are on the periphery of groups' home ranges, multiple groups may try to make use of them (usually at different times (although numerous intergroup encounters were observed in direct relation to contested food sources within overlapping areas)). This was particularly true during winter when areas that contained hawthorn bushes (and berries) were contested by the Green and Purple groups almost daily for a period of weeks. Indeed, an independent 2 sample t-test comparing the mean productivity value of areas in and outside overlap zones indicated that areas of home range overlap were on average more productive than areas used by single groups only.

It is also possible that the preference for feeding in overlapping areas was driven by the large amount of time that the Blue and Yellow groups spent waiting for provisioning by the road within the (large) shared portion of their home ranges. However, when the feeding resource selection model was rerun without these groups the preference for overlapping areas remained significant. Interestingly however when the Blue and Yellow groups were removed from the analysis the model results indicated a general avoidance of areas close to roads. This, in conjunction with the finding that overlapping areas were on average more productive, supports the idea that macaques choose the most productive areas available to them to feed, even if they overlap the home ranges of other groups.

Both the change in road preference (when the Blue and Yellow groups were removed) and the preference for feeding in overlapping areas suggest interesting directions for future work. Firstly, by investigating the habitat selection of each group individually to assess the effects of varying degrees of exposure and habituation to human activity and infrastructure, and secondly, by investigating in greater detail how groups use, contest, and police overlapping home range areas. Few studies have focused on the effects of neighbouring groups on the behaviour of primates, but in those that have, overlapping zones are routinely reported to be under-used (Wrangham, Crofoot, Lundy, and Gilby, 2007). A limited number of studies have recorded primates making use of overlapping home range areas but no consistent pattern of use emerges. Verreaux's sifaka (*Propithecus verreauxi*) use overlapping zones but their behavioural patterns (specifically resting and foraging times) do not differ significantly from those observed in core areas (Benadi, Fichtel, and Kappeler, 2008). Aggressive intergroup encounters in some other species such as chimpanzees, Diana monkeys *(Cercopithecus diana*), and Stuhlmann's blue monkeys (*Cercopithecus mitis*) can result in the extensive wounding and even death of individuals (Wrangham, Wilson, and Muller, 2006; McGraw, Plavcan, and Adachi-Kanazawa, 2002; Payne, Lawes, and Henzi, 2003 respectively). However, such lethal aggression between groups is rare in Barbary macaques (Deag, 1975), and the groups studied here seem largely willing to use overlapping areas, not only for feeding (as might be expected when productivity is high), but also for resting behaviour. All of which suggests that macaques may perceive overlap zones as both high reward and low risk areas; a hypothesis that could be tested further by examining duration of stay, other activity patterns, use of food resources, use of sleeping sites, group cohesion, and the frequency of tree-shaking behaviour.

3.4.2.2 Resting behaviour

Resting macaques avoided open areas and herding routes generally. This is unsurprising given that most primates spend their inactive periods in/on trees, cliffs, or other natural structures (see Anderson, 1984 for review), and that the tallest, broadest trees within the study area are found in areas of dense and moderate forest cover. This behaviour has been interpreted as a means of reducing risk from terrestrial predators (Anderson, 1984); and of the limited predatory threats facing the macaque population in INP (see section 2.2.1 for details) the majority are terrestrial. As such, any activity during which alertness is reduced (such as resting/sleeping) is more safely carried out in the trees. Indeed, 62% of all hourly scans in which an individual was resting were classed as low-storey or higher (see methods for definitions) (mean absolute height in metres±SE: 12.9±0.2, the highest percentage and mean absolute height of the 4 behaviours examined). Bonnet macaques (*Macaca radiata*) adopt a similar strategy when choosing sleeping trees, selecting the most difficult sites for predators to access such as tall, emergent trees that typically overhang water (Ramakrishnan and Coss, 2001). Other semi-terrestrial species (as the Barbary macaque) such as the chacma baboon also select tall trees or steep cliffs as sleeping sites (Hall, 1963).

Unexpectedly however, resting macaques showed a preference for areas that overlapped the home ranges of other groups. A similar tendency was observed among long-tailed macaques in Bali Barat National Park, Indonesia (although the study only involved 1 group). The group was found to favour particular sleeping areas despite the fact that frequent, agonistic intergroup encounters occurred at those sites (Brotcorne et al., 2014). Moustached tamarin (*Saguinus mystax*) groups also tend to choose sleeping sites located in overlapping areas of their home ranges (Ramirez, 1989). Such behaviour is in contrast to that reported in several other primate studies where monkeys preferentially slept in non-overlapping areas of their home range (e.g. *Colobus guereza* - Von Hippel, 1998; e.g. *Hylobates pileatus* - Phoonjampa, Koenig, Borries, Gale, and Savini, 2010; e.g. *Trachypithecus leucocephalus* - Dayong, Qihai, Xiaoping, Henglian, and Chengming, 2011). Dayong et al. (2011) suggest that by choosing sleeping sites on the periphery of a home range, primates may detect neighbouring groups earlier, making range defence easier. Given that 67% (n=39) of all recorded intergroup encounters in this study took place in areas of home range overlap it is possible that macaques may prefer to rest/sleep in these overlapping areas, in part, as a means of ensuring early detection of other groups.

However, it seems more likely that they primarily select overlapping home range areas to feed in (overlapping areas being on average more productive) and subsequently rest there following that feeding activity. This may also explain why macaques selected areas close to roads when resting. It may be that macaques preferentially rest in areas close to roads before and/or after roadside provisioning in order to maximise the chances of receiving human food; a supposition supported by both the feeding and socialising road proximity results. Indeed, although it failed to reach statistical significance, macaques also showed a preference for areas of home range overlap when socialising (an activity that is frequently observed in association with resting behaviour and following long bouts of feeding behaviour).

3.4.2.3 Social behaviour

Macaques avoided open areas and herding routes during social behaviour, and preferred areas close to roads. A great deal of the social behaviour observed in this study comprised time spent grooming (85% of all social behaviour scans comprised grooming behaviours), an activity that (like resting) is characterised by a decrease in alertness (particularly on the part of receivers who were frequently observed with their eyes closed during/throughout long grooming bouts). It is unsurprising therefore that macaques avoided both open areas and areas close to herding routes during social behaviour; most likely for the same reasons discussed above, i.e. to reduce the risk of predation or disturbance. More challenging to explain however is the avoidance of high productivity areas, particularly given the fact that grooming bouts would regularly occur directly after extended periods of feeding activity (in addition to the predictable post-waking / pre-sleeping grooming bouts). This preference is unlikely to be explained by the contribution of play or sexual behaviour to the social behaviour class given that, as described above, in 85% of social behaviour scans macaques were engaged in grooming behaviour. One possible explanation that warrants further investigation is that macaques prefer particular micro-habitat features (defined at a finer scale than examined here) for social behaviour that are inconsistent with certain high productivity areas, e.g. tree species availability, width, and height, canopy connection, distance from forest edge etc. Few primate studies have examined micro-habitat preference in relation to social behaviour, however Akers, Islam, and Nijman (2013) found that western hoolock gibbons (*Hoolock hoolock*) preferentially used interior forest habitat with low food tree availability when sleeping and socialising (as did macaques engaged in social behaviour in this study).

3.4.2.4 Travel behaviour

The habitat preferences of macaques when travelling stand out from those of the other behaviours examined in this study, most notably in relation to their use of areas close to herding routes. Groups avoided open areas when travelling, preferring densely forested areas (presumably to reduce the risk of harassment by dogs and/or humans, as discussed previously). Groups also preferred steep slopes when travelling, a finding that may be explained in part by the distinctive way in which they tend to travel. Groups often covered large distances at speed, remaining in one area until movement was initiated, after which they would move rapidly (and linearly) to their next destination. Travelling groups would frequently proceed in a very linear manner, ascending, descending, and traversing rugged terrain with little apparent difficulty (as might be the case for humans). For example, the Purple group's home range covers a very large area (4.26 km^2; 0.11 km^2 per individual) of considerable geographic and altitudinal diversity. Elevation ranges from 1500 to 1823 m.a.s.l., and when the group travels between preferred sites they frequently have to surmount steep cliffs and gorges; it is unsurprising therefore that a 'preference' for steep slopes is exhibited when travelling. The Red group face a similar situation given that their home range is significantly overlapped by that of the Purple; 53.6% of their range is shared with the Purple group, including much of the steep and rugged terrain. The geography of the Green group's home range also requires that they travel over steep terrain when moving between discontinuous core areas. The group often occupies 2 relatively isolated areas at the 'top' (1849 and 1916 m.a.s.l.) of their home range for days at a time, travelling very little until descending (often very rapidly) to their other preferred core area near the road (1752 m.a.s.l.). These journeys usually take place along predictable and well-used routes that make use of the steep sided valleys that cover much of the Green group’s home range. The Yellow group’s home range is almost entirely flat, but the Blue group’s travel behaviour follows a similar pattern to that of the Green. Their home range also spans a broad elevation range (1719 to 1873 m.a.s.l.) and although they spend most of their time at the flat tourist site at Agdal, when they do depart they tend to move very rapidly, following an almost straight path to the other heavily used part of their home range, a route which is again both predictable and requires several steep ascents and descents.

It has been suggested in other species that slopes can provide increased security for individuals by increasing detection range (as a result of increased visibility and olfactory range). However, these findings apply to grizzly and brown bears (Apps, McLellan, Woods, and Proctor, 2004; Martin et al., 2010), animals with a highly developed sense of smell (Herrero, 1985), unlike primates (with the exception of the nocturnal strepsirhines), including the Barbary macaque (Preuschoft and Preuschoft, 1994). It is therefore more likely that steep slopes are not ‘selected’ (in a preferential sense) by macaques when travelling, but that in moving in as linear a travel path as possible groups encounter and are willing to negotiate steep slopes.

This tendency to travel in a rapid, linear manner may also explain the other unusual observation that unlike the other behaviours examined, macaques do not show a general avoidance of areas close to herding routes when travelling; they only avoid herding routes when habitual activity is moderate or high. It may be that that it is more time and energy efficient for macaques to travel on herding routes than the forest, and therefore that groups are willing to pass through potentially risky areas, but only when human activity is habitually low. The potential risks could be diminished further if groups move through risky areas at high speed (as observed in African elephants that increase travel speed when passing through human-dominated areas (Graham et al., 2009)), something that could be examined in closer detail moving forward. Both potential explanations suggest that macaque travel patterns largely reflect the most efficient route from A to B (in terms of linearity and/or difficulty of travel), rather than an active selection/avoidance of areas.

3.4.3 Conclusions

The importance of human activity and infrastructure for the persistence of the Barbary macaque in INP, and in the wild more generally, differs with spatio-temporal scale. At the landscape (or population) level the few remaining macaque populations occur in areas of relatively low human density, e.g. the cedar forests of the Middle and High Atlas Mountains, the Rif Mountains in the north of Morocco, and the Tellian Atlas Mountains and Chréa National Park in Algeria (Fa, Taub, Ménard, and Stewart, 1984; Scheffrahn, Ménard, Vallet, and Gaci, 1993; Ciani et al., 2005). However, human activities increasingly impact these landscapes, and given the mounting needs of expanding human populations this influence is unlikely to abate or recede. As such, macaques are increasingly unable to avoid some degree of overlap between their home ranges and human activities and infrastructure. The macaques in this study appear to deal with this in 2 ways. First, they avoid areas of habitual herding route activity (presumably in an attempt to minimise the possibility of encountering dogs), a behaviour that is more pronounced (during feeding behaviour) as human activity increases. Second, they select areas close to roads in general (with the exception of travel behaviour), presumably in an attempt to acquire the calorie-dense human food that is often given to them by passing motorists and/or tourists. This behaviour also differs according to levels of human activity. When feeding, macaques do not exhibit the same general preference for areas close to roads, instead they prefer those areas only when road traffic is at moderate or high levels, presumably in an attempt to maximise the chances of receiving food. Thus there is a flexible spatio-temporal response to human activity and infrastructure by macaques.

These results, particularly those pertaining to road preference, suggest a considerable degree of habituation to human presence and activities that extends beyond the long-habituated “tourist-site” groups. The predictability of human activity within INP and the flexibility of the macaques’ response to it may allow these groups to persist in areas where human activity and infrastructure, and critical macaque habitat overlap. The results of this study highlight the importance of investigating temporal and behavioural variation in habitat selection. Failure to consider this variation can give rise to misleading conclusions about the effects of human activity and infrastructure, the results of which can hinder the effectiveness of conservation measures.

Chapter 4: General Discussion

The main aim of this study was to investigate how wild Barbary macaques respond to, and cope with, increasing levels of human disturbance (encounters, activities, and infrastructure) within Ifrane National Park, Morocco. As predicted, macaques adjusted both their short-term coping behaviour and long-term ranging behaviour in response to various levels and types of human disturbance. In response to human/dog encounters, macaque behaviour appeared to track short term changes in the perceived risk/reward balance, i.e. responses to disturbance were proportional to the perceived risk/reward of the situation. A similarly flexible strategy was observed in terms of habitat use. Macaques not only altered their ranging patterns in space and time (in association with human activity, infrastructure, and intensity of use) but also over/under-used particular areas of their home ranges when engaged in certain behaviours.

This is (to my knowledge) the first attempt to quantify the immediate behavioural responses of wild Barbary macaques to the presence of potential predators (dogs), or indeed to any human encounter other than those with tourists. It appears that macaques make use of a similar suite of behaviours in response to both encounter types. The behaviours observed in association with potentially threatening encounters allow macaques to trade-off the energetic and lost opportunity costs of escaping predators against the higher potential cost of injury or death; whilst the behaviours observed in association with provisioning encounters allow macaques to trade-off the potential costs of increased intragroup conflict (and increased proximity to humans) against the energetic benefits of consuming calorie-dense human food.

The way in which macaques alter their habitat use in response to human activity and infrastructure appears to serve a similar function, allowing macaques to minimise the risks and maximise the benefits associated with human activity. Macaques can avoid unwanted encounters by staying away from sites/routes that are commonly used by humans/dogs and/or only using those areas when the probability of an encounter is low. While this may minimise the potential costs associated with risky areas, wildlife that avoid them often suffer similar costs to those imposed by habitat loss or degradation because they underuse resources from those areas (Gill and Sutherland, 2000; Gill, Sutherland, and Watkinson, 1996). However, by selecting areas close to roads (the loci for human provisioning) and/or frequenting those areas when the risk/benefit balance of roadside provisioning is most heavily in their favour, macaques can increase the probable frequency of provisioning encounters, and in doing so offset some of the potential costs of avoiding other perceived risky areas.

Despite the difference in their proximate functions, both the short-term behavioural and longer-term habitat use strategies may ultimately allow macaques to modulate the potential costs and benefits of anthropogenic encounters. This convergence of purpose supports the broader idea that these behaviours (among others) may be components of a general coping strategy, particularly (but not exclusively (Weschler, 1995)) utilised by primates to offset some of the costs associated with human disturbance (Gustison et al., 2012; Van Wolkenten et al., 2006; Wittig et al., 2008).

The primary contribution of this study is to improve our understanding of how animals that are constrained to stay in disturbed areas attempt to manage those costs. Gill et al. (2001) predict that habitat shifts will not occur if alternative habitats are too distant or of too low quality to make change profitable. However they make no predictions about the potential responses of animals that are trapped inside fragmented patches of suitable habitat (as are the study groups), only stating that they must suffer the costs in terms of reduced survival or reproductive success. The changes observed in this study suggest that in lieu of emigration, (trapped) animals may have to adopt other strategies to cope with encroaching human influence. Specifically, they may a) alter the way in which they use their home ranges, exploiting human resources where possible whilst avoiding potential threats, and b) (where encounters are unavoidable) employ a variety of coping strategies that buffer the negative consequences of human encounters whilst allowing them (where possible) to exploit such encounters.

4.1 Implications for wildlife conservation

Understanding wildlife responses to shifting patterns of resource availability and risk is an important conservation goal, particularly when the fate of many wildlife populations depends on their capacity to coexist with humans. The initial response of wildlife to human development/disturbance is typically a change in behaviour. This change can occur at several scales, ranging from short-term alterations in activity budget (Altmann and Muruthi, 1988; Hejcmanová et al., 2013; Unwin and Smith, 2010) to large scale emigration or habitat-use change (Bouyer et al., 2015; Hebblewhite and Merrill, 2008; Martin et al., 2010). However, in order to make accurate and effective conservation recommendations it is important that a lack of habitat shift is not interpreted as a lack of disturbance impact (Gill et al., 2001). Animals that do not shift habitats may simply have no alternative place worth going to. If wildlife management is to succeed in reducing/avoiding human-wildlife conflict it is essential to understand how animals perceive these risks and benefits, how they balance them, which conditions most modify their behaviour, and whether these changes affect survival and/or fecundity (and thus population size) (Gill et al., 2001).

This is particularly relevant when dealing with endangered species, many of which are so because of declining habitat availability and quality (Ceballos et al., 2015). In such cases we may examine changes in habitat use and activity to best gauge a) the impacts of human disturbance on trapped animals, b) which disturbances impact animals most severely, and c) which areas/problems require the most immediate conservation and management action. If we do not there is a risk that limited conservation resources will be misspent and the often limited will to address conservation issues misdirected. The results of this study highlight the value and importance of considering the effects of multiple different types of human activity and infrastructure (at different spatio-temporal scales) on wildlife behaviour and welfare.

Given that the Barbary macaque population is declining (Butynski et al., 2008; Ménard et al., 2014a), and that human disturbance is implicated as a probable cause, a great deal of research effort has been expended towards the protection of this species (see below). This work has generated a wide range of conservation recommendations, many of which are supported by the findings of this study. The key recommendations include: the reduction of deforestation and habitat deterioration (Ciani et al., 2005; Waters, Aksissou, Harrad, Hobbelink, and Fa, 2007); the control of overgrazing by livestock, the erection and maintenance of fenced, protected areas within remaining forests, and the promotion of sustainable forest use practices within Morocco (Ciani et al., 2005); the reduction of poaching and an increase in law enforcement (Ménard et al., 2014a; Van Lavieren and Wich, 2009); the reduction/elimination/regulation of human provisioning (El Alami, Van Lavieren, Rachida, and Chait, 2012; Maréchal et al., 2011; Maréchal, Semple, Majolo, and MacLarnon, 2016); and the better management of tourist-macaque interactions (Maréchal et al., 2011; Ménard et al., 2014a); all of which are included in the Barbary Macaque Action Plan (2012), the actual, practical application of which would serve to address all of these concerns.

However, rather than repeating in detail these same recommendations I present instead 3 recommendations unique to the results of this study:

1. Because macaques were found to generally favour areas close to roads, steps should be taken to slow traffic passing through macaque habitat, and to properly manage the roadside lay-bys and tourist sites from which the most reckless provisioning occurs. Not only would this reduce the likelihood of collisions (with macaques and other vehicles) but it may also reduce the negative impacts that provisioning has on macaque health (Maréchal et al., 2016) and help to slow the trend of increasing habituation to humans; a process that grossly exacerbates the poaching problem that threatens the species' continued existence (Ménard et al. 2014a).

Three signs warning motorists about macaques on the road were erected by the Moroccan High Commission for Water, Forests and Desertification (in conjunction with the non-governmental organisation (NGO) Moroccan Primate Conservation (MPC)) in 2014, but to no avail (personal observation – macaque road deaths continued and average traffic speeds appeared to remain the same). Similarly, talks took place between MPC and the local branch of the 'High Commission' regarding the use of traffic calming measures (specifically, small concrete mounds placed across the width of roads), but this option was rejected due to the designation of the road as a national traffic route (analogous to an A road in the United Kingdom). Indeed, in direct opposition to invited conservation recommendations, prior to the end of this study construction work began in order to widen the road. The incursion of roads into wildlife habitat is a powerful driver of multiple other deleterious effects, including road kill, increased ease of access for loggers and poachers, increased habituation to humans, and increased reliance on human food (Kerley et al., 2002), however there appears to be little will to address this problem within INP at present.

2. Any further expansion of the herding routes within INP should be curtailed. At present the macaques can avoid herding routes within their home ranges in space and time; however this may not be a sustainable strategy if routes expand in size and number. Given the observed reliance on escape behaviour (flight to the trees) by macaques in response to dog encounters any further reduction in tree cover (and/or widening of herding routes) may render macaques more vulnerable to dog predation, which may in turn restrict their already limited ability to move between fragmented forest patches. The Barbary macaque in Morocco is already limited in range, partly as a result of the ubiquitous presence of humans and livestock (Fa, 1986a), and one of the principal threats to their survival is competition for understory forage with the livestock that share their

habitat (Ménard et al., 2014a). Whilst macaques may be able to avoid/manage actual human/dog encounters, any increase in the volume of overgrazing could exacerbate the species' decline by other means.

3. Any planning directed towards the creation of wildlife corridors should take into account behaviour-specific variation in habitat selection. Information concerning the habitat conditions that are selected/avoided by macaques when travelling can be important when designing wildlife corridors. For example, the results of this study indicate that macaques avoid open areas when travelling in favour of dense forest; that they may be prepared to navigate areas close to herding routes at certain times when human activity is low; and perhaps most significantly, that they are not averse to travelling on steep slopes. It may be that corridors could make use of steeply sloping terrain that humans may otherwise avoid or have little use for, neutralising the potential for conflict over shared space with pastoralists, and diminishing the likelihood of human-macaque encounters.

The Moroccan High Commission for Water, Forests and Desertification Control has taken many positive steps (in conjunction with NGOs such as MPC and Barbary Macaque Awareness & Conservation) towards safeguarding the future of the Barbary macaque in Morocco, however much more remains to be done. Recent work on Barbary macaque behaviour continues to highlight the extent of their behavioural flexibility, demonstrating for example that they have the ability to vary their diet in order in order to exploit different anthropogenic food sources in expanding peri-urban zones (Maibeche, Moali, Yahi, and Ménard, 2015), and that they vary their grooming behaviour according to kinship, rank, and friendship (Roubová, Konečná, Šmilauer, and Wallner, 2015). This study further illustrates the extent of their behavioural flexibility by demonstrating that macaques are able to adjust their ranging and coping behaviours in response to various levels and types of human disturbance. The ability to do so may be the key that allows wildlife to hang-on (at least until vigorous conservation measures are enacted) in areas where human activity and critical habitat overlap. Findings such as these can enhance our understanding of (and ability to manage) the impacts of increasing human expansion into wildlife habitat, whilst further research could build on these results to gain a better understanding of the ultimate consequences (for macaque population dynamics) of the observed spatial, temporal, and behavioural changes associated with human disturbance.

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Appendix A - Table 1. Results of the GLMMs testing the relationships between encounter type and escape behaviour.

			Escape Behaviours											
			Tree ascent rate				**Proportion of time in trees**				**Flight rate**			
		Null vs. full model	**N**	**df**	χ^2	***p*-value**	**N**	**df**	χ^2	***p*-value**	**N**	**df**	χ^2	***p*-value**
			104	17	91.653	**<0.001**	104	17	71.374	**<0.001**	104	17	184.57	**<0.001**
		Intercept	**Est.**	**SE**	***t***	***p*-value**	**Est.**	**SE**	***t***	***p*-value**	**Est.**	**SE**	***t***	***p*-value**
			-0.507	0.366	-1.386	0.166	-4.969	1.317	-3.774	**<0.001**	-0.204	0.25	-0.817	0.414
Encounter Type	**‘Work’**	**Pre vs. During**	0.401	0.24	1.672	0.094	0.063	0.471	0.133	0.894	0.449	0.175	2.566	**0.01**
		Pre vs. Post	-0.142	0.235	-0.604	0.546	-0.531	0.5	-1.063	0.288	0.004	0.168	0.024	0.981
	‘Work-Dog’	**Pre vs. During**	1.349	0.448	3.01	**0.003**	3.678	1.22	3.015	**0.003**	0.56	0.329	1.704	0.088
		Pre vs. Post	0.69	0.506	1.363	0.173	2.74	1.432	1.913	0.056	-0.038	0.339	-0.111	0.911
	‘Dog-Solo’	**Pre vs. During**	0.99	0.361	2.741	**0.006**	4.486	0.837	5.361	**<0.001**	0.954	0.264	3.622	**<0.001**
		Pre vs. Post	0.716	0.364	1.968	**0.049**	5.262	0.896	5.874	**<0.001**	-0.017	0.25	-0.069	0.945
	‘Recreation’	**Pre vs. During**	-0.491	0.311	-1.579	0.114	0.968	0.646	1.499	0.134	-0.403	0.216	-1.866	0.062
		Pre vs. Post	-0.45	0.325	-1.383	0.167	1.1	0.68	1.617	0.106	0.01	0.225	0.045	0.964
	‘Recreation-Provisioned’	**Pre vs. During**	0.461	0.314	1.469	0.142	0.201	0.642	0.312	0.755	0.865	0.222	3.893	**<0.001**
		Pre vs. Post	0.168	0.32	0.525	0.6	1.572	0.715	2.2	**0.028**	0.114	0.223	0.511	0.609
		Group Size	0.011	0.009	1.171	0.242	-0.013	0.034	-0.397	0.691	0.004	0.006	0.573	0.566
		Max. Number of Anthropogenic Agents	0.008	0.012	0.644	0.519	0.021	0.044	0.477	0.634	0.019	0.008	2.23	**0.026**
		Home-range: Outer vs. Core	0.156	0.16	0.974	0.33	0.387	0.604	0.641	0.522	-0.053	0.112	-0.47	0.638
	Random effects		**Variance**		**Std. Dev.**		**Variance**		**Std. Dev.**		**Variance**		**Std. Dev.**	
	Focal observation : Subject		0.324		0.569		8.581		2.929		0.137		0.37	
	Subject		0.028		0.168		<0.001		<0.001		<0.001		<0.001	
	Residual		0.765		0.874		1.132		1.064		0.407		0.638	

Appendix A - Table 2. Results of the GLMMs testing the relationships between encounter type and affiliative behaviour.

			Affiliative Behaviours											
			Approach rate				Proximity (<1.5 m) proportion				Short affiliative behaviour rate			
		Null vs. full model	**N**	**df**	χ^2	***p*-value**	**N**	**df**	χ^2	***p*-value**	**N**	**df**	χ^2	***p*-value**
			104	17	34.684	**0.007**	104	17	33.434	**0.01**	104	17	47.519	**<0.001**
		Intercept	**Est.**	**SE**	***t***	***p*-value**	**Est.**	**SE**	***t***	***p*-value**	**Est.**	**SE**	***t***	***p*-value**
			1.362	0.478	2.85	**0.004**	-1.437	0.871	-1.651	0.099	1.461	0.466	3.133	**0.002**
Encounter Type	**'Work'**	**Pre vs. During**	-0.438	0.298	-1.469	0.142	-1.298	0.532	-2.44	**0.015**	-0.795	0.299	-2.656	**0.008**
		Pre vs. Post	0.775	0.311	2.491	**0.013**	-0.235	0.528	-0.444	0.657	-0.255	0.297	-0.756	0.45
	'Work-Dog'	**Pre vs. During**	1.053	0.587	1.793	0.073	2.324	1.018	2.284	**0.022**	0.625	0.53	1.179	0.239
		Pre vs. Post	1.182	0.651	1.816	0.069	2.958	1.215	2.435	**0.015**	1.914	0.605	3.165	**0.002**
	'Dog-Solo'	**Pre vs. During**	-0.13	0.448	-0.291	0.771	-0.49	0.792	-0.619	0.536	-0.085	0.418	-0.203	0.84
		Pre vs. Post	-0.746	0.483	-1.545	0.122	-0.886	0.829	-1.068	0.285	0.73	0.457	1.595	0.111
	'Recreation'	**Pre vs. During**	0.296	0.389	0.76	0.447	1.336	0.685	1.951	0.051	0.546	0.381	1.432	0.152
		Pre vs. Post	-0.813	0.431	-1.884	0.06	0.887	0.735	1.207	0.227	0.004	0.405	0.01	0.992
	'Recreation-Provisioned'	**Pre vs. During**	0.166	0.394	0.421	0.673	0.581	0.682	0.852	0.394	1.067	0.373	2.859	**0.004**
		Pre vs. Post	-0.912	0.44	-2.076	**0.038**	0.126	0.754	0.167	0.867	0.75	0.412	1.82	0.069
		Group Size	0.004	0.012	0.367	0.714	-0.015	0.022	-0.707	0.48	-0.006	0.011	-0.507	0.612
		Max. Number of Anthropogenic Agents	-0.001	0.015	-0.096	0.924	-0.024	0.029	-0.846	0.398	-0.005	0.015	-0.371	0.71
		Home-range: Outer vs. Core	0.2	0.202	0.991	0.322	0.653	0.39	1.674	0.094	0.111	0.197	0.562	0.574
	Random effects		**Variance**		**Std. Dev.**		**Variance**		**Std. Dev.**		**Variance**		**Std. Dev.**	
	Focal observation : Subject		0.417		0.646		3.388		1.841		0.516		0.718	
	Subject		0.068		0.262		<0.001		<0.001		0.067		0.259	
	Residual		0.8		0.894		1.236		1.112		0.89		0.943	

Appendix A - Table 3. Results of the GLMMs testing the relationships between encounter type and affiliative behaviour.

			Affiliative Behaviours							
			Allogroom rate				**Allogrooming proportion**			
		Null vs. full model	**N**	**df**	χ^2	***p*-value**	**N**	**df**	χ^2	***p*-value**
			104	17	30.216	**0.025**	104	17	37.087	0.003
		Intercept	**Est.**	**SE**	***t***	***p*-value**	**Est.**	**SE**	***t***	***p*-value**
			0.602	0.487	1.236	0.217	-4.195	0.907	-4.628	**<0.001**
Encounter Type	**'Work'**	**Pre vs. During**	-0.002	0.246	-0.008	0.994	-0.484	0.444	-1.09	0.275
		Pre vs. Post	0.442	0.262	1.688	0.091	0.117	0.515	0.227	0.821
	'Work-Dog'	**Pre vs. During**	0.895	0.477	1.875	0.061	2.268	0.846	2.68	**0.007**
		Pre vs. Post	0.755	0.536	1.407	0.159	2.247	1.108	2.029	**0.042**
	'Dog-Solo'	**Pre vs. During**	-0.326	0.361	-0.903	0.367	-0.364	0.67	-0.543	0.587
		Pre vs. Post	-0.161	0.395	-0.408	0.683	0.717	0.816	0.878	0.38
	'Recreation'	**Pre vs. During**	-0.252	0.32	-0.788	0.43	0.109	0.584	0.187	0.852
		Pre vs. Post	-0.218	0.366	-0.596	0.551	0.623	0.729	0.855	0.393
	'Recreation-Provisioned'	**Pre vs. During**	-0.284	0.32	-0.886	0.375	-0.418	0.599	-0.698	0.485
		Pre vs. Post	-0.842	0.359	-2.345	**0.019**	-1.283	0.717	-1.789	0.074
		Group Size	0.001	0.013	0.085	0.932	0.007	0.023	0.299	0.765
		Max. Number of Anthropogenic Agents	-0.006	0.015	-0.366	0.715	-0.019	0.03	-0.644	0.52
		Home-range: Outer vs. Core	0.402	0.208	1.934	0.053	0.809	0.404	2.002	**0.045**
	Random effects		**Variance**		**Std. Dev.**		**Variance**		**Std. Dev.**	
	Focal observation : Subject		0.5		0.707		3.708		1.926	
	Subject		0.12		0.347		0.356		0.596	
	Residual		0.714		0.845		1.33		1.153	

Appendix A - Table 4. Results of the GLMMs testing the relationships between encounter type and the number of partners (per hour) engaged in affiliative behaviours with the focal individual.

			Affiliative Behaviours											
			Approach and Proximity (Number of Partners)				**Short Affiliative Behaviours (Number of Partners)**				**Allogrooming (Number of Partners)**			
		Null vs. full model	**N**	**df**	χ^2	***p*-value**	**N**	**df**	χ^2	***p*-value**	**N**	**df**	χ^2	***p*-value**
			104	17	24.903	0.097	104	17	42.916	**<0.001**	104	17	27.253	0.054
		Intercept	**Est.**	**SE**	***t***	***p*-value**	**Est.**	**SE**	***t***	***p*-value**	**Est.**	**SE**	***t***	***p*-value**
			2.043	0.469	4.358	<0.001	1.132	0.426	2.658	**0.008**	0.612	0.448	1.366	0.172
Encounter Type	**'Work'**	**Pre vs. During**	-0.601	0.295	-2.04	0.041	-0.737	0.264	-2.793	**0.005**	-0.027	0.24	-0.111	0.912
		Pre vs. Post	-0.143	0.299	-0.479	0.632	-0.171	0.272	-0.629	0.53	0.396	0.254	1.557	0.119
	'Work-Dog'	**Pre vs. During**	1.113	0.551	2.02	0.043	0.587	0.479	1.224	0.221	0.909	0.475	1.913	0.056
		Pre vs. Post	1.516	0.609	2.487	0.013	1.548	0.546	2.837	**0.005**	0.521	0.525	0.992	0.321
	'Dog-Solo'	**Pre vs. During**	0.282	0.445	0.634	0.526	-0.013	0.372	-0.035	0.972	-0.29	0.356	-0.815	0.415
		Pre vs. Post	-0.291	0.469	-0.62	0.535	0.436	0.406	1.074	0.283	-0.247	0.384	-0.644	0.52
	'Recreation'	**Pre vs. During**	0.346	0.379	0.912	0.362	0.466	0.338	1.379	0.168	-0.16	0.314	-0.51	0.61
		Pre vs. Post	0.184	0.417	0.441	0.659	-0.104	0.366	-0.283	0.777	-0.039	0.357	-0.108	0.914
	'Recreation-Provisioned'	**Pre vs. During**	0.536	0.379	1.413	0.158	0.994	0.331	3.004	**0.003**	-0.291	0.312	-0.934	0.35
		Pre vs. Post	0.033	0.418	0.078	0.938	0.583	0.369	1.581	0.114	-0.815	0.35	-2.332	0.02
		Group Size	-0.005	0.012	-0.459	0.646	-0.003	0.01	-0.318	0.751	0.001	0.011	0.086	0.931
		Max. Number of Anthropogenic Agents	-0.001	0.015	-0.043	0.966	-0.005	0.013	-0.383	0.702	-0.011	0.014	-0.762	0.446
		Home-range: Outer vs. Core	0.477	0.206	2.316	0.021	0.12	0.178	0.673	0.501	0.323	0.191	1.692	0.091
	Random effects		**Variance**		**Std. Dev.**		**Variance**		**Std. Dev.**		**Variance**		**Std. Dev.**	
	Focal observation : Subject		0.459		0.678		0.387		0.622		0.43		0.656	
	Subject		0.07		0.265		0.05		0.223		0.093		0.304	
	Residual		0.789		0.888		0.758		0.871		0.719		0.848	

Appendix A - Table 5. Results of the GLMMs testing the relationships between encounter type and self-directed behaviour.

			Displacement Behaviours											
			Scratch rate				**Self-groom rate**				**Self-groom proportion**			
		Null vs. full model	**N**	**df**	χ^2	***p*-value**	**N**	**df**	χ^2	***p*-value**	**N**	**df**	χ^2	***p*-value**
			104	17	28.997	**0.035**	104	17	22.878	0.153	104	17	19.902	0.279
		Intercept	**Est.**	**SE**	***t***	***p*-value**	**Est.**	**SE**	***t***	***p*-value**	**Est.**	**SE**	***t***	***p*-value**
			1.697	0.492	3.449	**<0.001**	0.182	0.385	0.471	0.637	-6.292	0.726	-8.67	<0.001
Encounter Type	**'Work'**	**Pre vs. During**	-0.509	0.304	-1.676	0.094	0.125	0.228	0.55	0.582	0.146	0.357	0.41	0.682
		Pre vs. Post	-0.201	0.319	-0.631	0.528	0.3	0.239	1.255	0.209	0.307	0.393	0.78	0.436
	'Work-Dog'	**Pre vs. During**	0.703	0.688	1.021	0.307	0.67	0.448	1.495	0.135	0.988	0.757	1.304	0.192
		Pre vs. Post	0.936	0.646	1.45	0.147	0.158	0.477	0.332	0.74	1.207	0.943	1.28	0.2
	'Dog-Solo'	**Pre vs. During**	0.217	0.442	0.491	0.623	-0.074	0.333	-0.221	0.825	-0.352	0.533	-0.661	0.509
		Pre vs. Post	1.069	0.47	2.273	**0.023**	0.061	0.366	0.167	0.868	0.586	0.652	0.899	0.369
	'Recreation'	**Pre vs. During**	0.586	0.397	1.474	0.14	-0.262	0.297	-0.882	0.378	-0.348	0.486	-0.716	0.474
		Pre vs. Post	0.825	0.424	1.946	0.052	0.149	0.34	0.438	0.662	-0.061	0.561	-0.108	0.914
	'Recreation-Provisioned'	**Pre vs. During**	1.006	0.392	2.564	**0.01**	0.003	0.296	0.012	0.991	-0.158	0.496	-0.319	0.75
		Pre vs. Post	0.643	0.422	1.523	0.128	-0.005	0.331	-0.015	0.988	-0.038	0.582	-0.065	0.948
		Group Size	0.003	0.012	0.268	0.788	-0.002	0.01	-0.172	0.864	0.012	0.018	0.648	0.517
		Max. Number of Anthropogenic Agents	0.007	0.016	0.473	0.636	-0.011	0.013	-0.85	0.396	-0.023	0.024	-0.933	0.351
		Home-range: Outer vs. Core	0.305	0.217	1.41	0.159	0.287	0.171	1.678	0.093	0.438	0.329	1.334	0.182
	Random effects		**Variance**		**Std. Dev.**		**Variance**		**Std. Dev.**		**Variance**		**Std. Dev.**	
	Focal observation : Subject		0.602		0.776		0.415		0.645		2.566		1.602	
	Subject		0.034		0.185		<0.001		<0.001		<0.001		<0.001	
	Residual		0.86		0.927		0.721		0.849		1.294		1.137	

Appendix B - Table 1. Summary of results from generalised linear mixed models for behaviour-specific resource selection function models (Feed and Rest). Statistically significant (α=0.05) *p*-values are underlined and in bold type.

Variable	**Model**									
	Feed					**Rest**				
	β	**SE**	**95% CI**	***z***	***p*-value**	**β**	**SE**	**95% CI**	**z**	***p*-value**
Intercept	-8.569	0.165	-8.892 , -8.246	-51.967	**<0.001**	-5.953	0.162	-6.27 , -5.635	-36.752	**<0.001**
Cover-Moderate	0.121	0.094	-0.063 , 0.305	1.29	0.197	-0.209	0.176	-0.553 , 0.135	-1.189	0.235
Cover-Open	-0.439	0.073	-0.582 , -0.295	-5.991	**<0.001**	-1.099	0.15	-1.392 , -0.806	-7.348	**<0.001**
Slope	0.044	0.027	-0.01 , 0.098	1.612	0.107	0.056	0.043	-0.028 , 0.14	1.315	0.188
Productivity	0.079	0.026	0.028 , 0.13	3.028	**0.002**	-0.064	0.043	-0.149 , 0.021	-1.483	0.138
Home Range Overlap (1)	0.33	0.058	0.216 , 0.444	5.685	**<0.001**	0.217	0.09	0.041 , 0.394	2.412	**0.016**
Herding route intensity of use (Moderate)	0.033	0.179	-0.318 , 0.384	0.185	0.853	0.819	0.165	0.497 , 1.142	4.978	**<0.001**
Herding route intensity of use (High)	0.013	0.166	-0.313 , 0.339	0.077	0.939	0.427	0.158	0.117 , 0.738	2.696	**0.007**
Distance-from-herding route	0.149	0.06	0.031 , 0.267	2.468	**0.014**	0.275	0.101	0.076 , 0.474	2.708	**0.007**
Road intensity of use (Moderate)	0.595	0.17	0.261 , 0.929	3.49	**<0.001**	0.91	0.158	0.6 , 1.22	5.754	**<0.001**
Road intensity of use (High)	0.224	0.175	-0.118 , 0.566	1.282	0.2	0.395	0.163	0.076 , 0.714	2.425	**0.015**
Distance-from-road	0.035	0.055	-0.072 , 0.143	0.648	0.517	-0.226	0.094	-0.411 , -0.041	-2.397	**0.017**
Herding route density	0.103	0.077	-0.049 , 0.254	1.332	0.183	0.179	0.073	0.035 , 0.322	2.445	**0.014**
Road density	0.078	0.068	-0.055 , 0.211	1.149	0.25	-0.098	0.076	-0.247 , 0.051	-1.287	0.198
Herding route intensity of use (Moderate) x Distance-from-herding route	0.237	0.072	0.095 , 0.378	3.271	**0.001**	0.075	0.115	-0.151 , 0.301	0.654	0.513
Herding route intensity of use (High) x Distance-from-herding route	0.258	0.069	0.122 , 0.394	3.727	**<0.001**	0.001	0.121	-0.236 , 0.237	0.006	0.995
Road intensity of use (Moderate) x Distance-from-road	-0.223	0.062	-0.345 , -0.1	-3.566	**<0.001**	-0.063	0.108	-0.275 , 0.149	-0.581	0.561
Road intensity of use (High) x Distance-from-road	-0.206	0.065	-0.334 , -0.078	-3.143	**0.002**	-0.207	0.12	-0.442 , 0.027	-1.732	0.083

Random effects	**Variance**	**Std. Deviation**	**Variance**	**Std. Deviation**
Subject : Scan : Group	0.044	0.209	2.648e-13	5.146e-07
Scan : Group	47.009	6.856	9.544	3.091
Group	<0.001	<0.001	3.635e-18	1.907e-09

Appendix B - Table 2. Summary of results from two generalised linear mixed models for behaviour-specific resource selection function models (Social and Travel). Statistically significant (α=0.05) *p*-values are underlined and in bold type.

Variable	**Model**									
	Social					**Travel**				
	β	**SE**	**95% CI**	***z***	***p*-value**	**β**	**SE**	**95% CI**	**z**	***p*-value**
Intercept	-5.146	0.113	-5.369 , -4.924	-45.357	**<0.001**	-4.55	0.125	-4.795 , -4.306	-36.519	**<0.001**
Cover-Moderate	-0.148	0.113	-0.369 , 0.073	-1.311	0.19	-0.228	0.15	-0.523 , 0.067	-1.515	0.13
Cover-Open	-0.877	0.091	-1.055 , -0.699	-9.659	**<0.001**	-0.773	0.116	-1 , -0.545	-6.652	**<0.001**
Slope	0.004	0.03	-0.056 , 0.063	0.12	0.905	0.105	0.038	0.03 , 0.18	2.754	**0.006**
Productivity	-0.128	0.03	-0.187 , -0.069	-4.274	**<0.001**	-0.064	0.038	-0.139 , 0.01	-1.689	0.091
Home Range Overlap (1)	0.079	0.062	-0.043 , 0.201	1.266	0.206	-0.145	0.078	-0.297 , 0.008	-1.861	0.063
Herding route intensity of use (Moderate)	0.523	0.121	0.286 , 0.759	4.329	**<0.001**	0.062	0.134	-0.201 , 0.325	0.462	0.644
Herding route intensity of use (High)	0.22	0.115	-0.006 , 0.446	1.907	0.056	-0.002	0.123	-0.243 , 0.239	-0.017	0.987
Distance-from-herding route	0.294	0.068	0.162 , 0.427	4.349	**<0.001**	0.031	0.08	-0.126 , 0.187	0.383	0.702
Road intensity of use (Moderate)	1.022	0.117	0.793 , 1.25	8.768	**<0.001**	0.532	0.129	0.279 , 0.786	4.118	**<0.001**
Road intensity of use (High)	0.404	0.12	0.169 , 0.639	3.373	**0.001**	0.399	0.128	0.149 , 0.649	3.125	**0.002**
Distance-from-road	-0.208	0.063	-0.332 , -0.085	-3.3	**0.001**	-0.14	0.074	-0.285 , 0.004	-1.906	0.057
Herding route density	0.148	0.054	0.041 , 0.254	2.723	**0.006**	0.077	0.061	-0.043 , 0.197	1.255	0.209
Road density	-0.07	0.049	-0.166 , 0.026	-1.42	0.156	-0.055	0.054	-0.161 , 0.051	-1.014	0.311
Herding route intensity of use (Moderate) x Distance-from-herding route	0.042	0.077	-0.11 , 0.194	0.543	0.587	0.25	0.1	0.053 , 0.446	2.493	**0.013**
Herding route intensity of use (High) x Distance-from-herding route	0.103	0.077	-0.048 , 0.255	1.339	0.181	0.227	0.094	0.043 , 0.412	2.42	**0.016**
Road intensity of use (Moderate) x Distance-from-road	-0.039	0.071	-0.177 , 0.1	-0.548	0.583	-0.027	0.09	-0.203 , 0.15	-0.297	0.767
Road intensity of use (High) x Distance-from-road	-0.085	0.077	-0.237 , 0.066	-1.109	0.268	-0.142	0.093	-0.325 , 0.041	-1.517	0.129

Random effects	**Variance**	**Std. Deviation**	**Variance**	**Std. Deviation**
Subject : Scan : Group	9.324e-09	9.656e-05	0.206	0.454
Scan : Group	7.082	2.661	6.653	2.579
Group	<0.001	<0.001	<0.001	<0.001