ETHNOPRIMATOLOGY OF *Macaca tonkeana*: THE INTERFACE OF PRIMATE ECOLOGY, HUMAN ECOLOGY, AND CONSERVATION IN LORE LINDU NATIONAL PARK, SULAWESI, INDONESIA

by

ERIN PHELPS RILEY

(Under the direction of Carolyn L. Ehardt)

ABSTRACT

This dissertation investigated the ecological and cultural interconnections between Tonkean macaques (*Macaca tonkeana*) and human residents of the Lindu valley in Lore Lindu National Park. The research had two major foci. The first examined how Tonkean macaques respond, in terms of their diet, activity patterns, and ranging patterns, to anthropogenic habitat alteration. The second assessed how human ecology affects the conservation of Tonkean macaques by examining (1) the conservation implications of overlapping resource use between Tonkean macaques and villagers in Lindu, and (2) how villagers' conceptualizations of forests, monkeys and protected areas impact conservation in the park. Two macaque groups, occupying habitats with different levels of anthropogenic alteration, were studied. Tree abundance, density of key food species, and fruit production were found to be greater in the minimally-altered habitat, substantiating the characterization of this habitat as higher quality. Tonkean macaques appear to respond to anthropogenic habitat alteration, and decreased habitat quality, by being flexible in their diet by incorporating more alternative food items and relying on resources that dominate human-altered areas, and by adjusting their activity budgets and use of space to increase their foraging effort. There was considerable overlapping use of forest resources between macaques and villagers, which may negatively impact the survival of macaques in human-modified environments. Macaque use of anthropogenic foods (e.g., cacao fruits, *Theobroma cacao*) was found to be nominal compared to other crop raiding animals, despite villagers' perceptions of the macaques as the most destructive animals. Considerable diversity was found within the local community of Tomado on knowledge, attitudes, and perceptions of the forest and its conservation, that varied by ethnic and cultural-ecological identity. The indigenous Lindu possess folklore that envisions monkeys and humans as interrelated biologically, ecologically, and culturally. This folklore results in tolerance of the macaques, and therefore may help to ensure their persistence. Overall, the research demonstrates the value of an integrated approach, such as ethnoprimatology, in understanding the behavioral flexibility of nonhuman primates that live in human-modified environments, and the key factors that affect conservation in areas where human and nonhuman primate needs are increasingly interwoven.

INDEX WORDS: Ethnoprimatology, Anthropogenic habitat alteration, *Macaca tonkeana*, Primate ecology, Diet, Ranging, Crop raiding, Conservation, Folklore, Sulawesi, Indonesia

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DEDICATION

Kepada masyarakat di Lindu

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

The project presented in this dissertation investigates the ecological and cultural interconnections between human and nonhuman primate inhabitants of the Lindu valley enclave in Lore Lindu National Park, Central Sulawesi, Indonesia. The project has both fundamental and applied significance. The fundamental significance lies in its contribution to a comparative socioecology of the genus *Macaca*, and our understanding of the behavioral and ecological plasticity of nonhuman primate populations that live in human-altered environments. The applied significance of the project rests in the contributions it will make to conservation management plans for Lore Lindu National Park.

Socioecology seeks to understand the relationship between ecology and social behavior in primates by characterizing the nature of the animal's environment and then hypothesizing how this environment shapes its social behavior. A recent and increasingly prevalent area of interest in this paradigm is the impact of humans, predominantly in the form of habitat alteration and/or destruction, on nonhuman primate ecology and social behavior (Janson, 2000). An extension of this concern (i.e., inclusion of the human dimension) is evident in the emergence of the new field of ethnoprimatology, which explicitly addresses the interface of cultural anthropology, primate behavior, and conservation (Sponsel, 1997). Increasingly, in many areas of the world (e.g., Africa, Asia and Southeast Asia), nonhuman primates and humans occur in very close proximity, exploiting common features of the environment. This results in situations where there is a strong potential for conflict[1]. Human proximity can have serious implications for the ecology and conservation of nonhuman primates, and research should be directed toward understanding what factors allow different primate species to persist under these potentially challenging conditions. Humans must also endure the consequences of such proximity and find ways of dealing with conflict; methods which may threaten the long-term conservation status of the nonhuman primates. Furthermore, human-nonhuman primate conflict often occurs in the context of protected areas (e.g., National Parks), where local villagers must comply with restricted use/access policies, thus perpetuating negative attitudes towards the protected area (and the wildlife it hosts) and potentially encouraging "illegal" land conversion and poaching (Barnes et al., 1992; van Kooten & Bulte, 2000). It is therefore critical that research, which occurs within the context of protected areas, address both sides of the conflict; that is, examining how nonhuman primates respond to human-induced habitat alteration and how the behavior and ecology of protected species, as well as conservation policy, affect the livelihoods of local human residents.

This dissertation contributes to the new field of ethnoprimatology by examining the interface of macaque ecology, human ecology, and conservation in Lore Lindu National Park (LLNP), Sulawesi, Indonesia. Using the "human-nonhuman primate community" as the primary unit of investigation, I employed a broadened community ecology approach that is concerned with the interconnections between human and nonhuman primates as members of an ecological community. Such an approach can elucidate the proximate effects of human influence (Bishop et al., 1981) on the ecology of nonhuman primates, the extrinsic factors[2] (i.e., human ecology)

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[1] I use the concept "conflict" here to mean negative interactions between human and nonhuman primates.

[2] Although I consider humans and nonhuman primates in such contexts as members of a community, I use "extrinsic" here to differentiate from genetic, ecological, and behavioral factors that are intrinsic to nonhuman primates.

that may be important determinants of the long-term conservation status of these primates, and the impact of human-nonhuman primate proximity on human livelihoods. The human-nonhuman primate community that I examined includes human residents of the villages of Tomado and Anca and the Tonkean macaques (*Macaca tonkeana*) that border these villages in the Lake Lindu valley enclave in Lore Lindu National Park (see Riley, in prep. a). Two overall research questions guided this dissertation:

(1) How does anthropogenic habitat alteration affect the foraging/feeding patterns, diet composition, activity patterns, ranging patterns, and habitat use of *M. tonkeana*?

(2) How does local human ecology affect the ability of *M. tonkeana* to persist in LLNP?

In this chapter, I contextualize the entire study within the existing literature on the ecological and behavioral flexibility of primates in response to habitat alteration, implications of human-nonhuman primate sympatry, and human dimensions of conservation. I give a detailed description of the research setting, including the field site and the human-nonhuman primate community studied. I then provide an overview of the research goals specific to each of the subsequent chapters, which are written as journal article manuscripts and constitute the core of the dissertation. Lastly, I present a general overview of the methods that I used during the study.

Research context

The three major threats to the persistence of wild nonhuman primate populations include habitat destruction, hunting, and live capture for export or local trade (Mittermeier & Cheney, 1987). While the loss of undisturbed habitat is widely recognized as the most serious threat to the survival of rain forest primates (Marsh et al., 1987), what is meant by "disturbance" and our understanding of the differential effects of varying types of disturbance on particular primate species are often not clear. The treatment of the concept of "human disturbance" as unnatural in the conservation literature (e.g., Soulé, 1995) has two major implications for the way in which we think about human-environmental interactions. First, it implies that humans are separate from their natural environment. Agrawal & Gibson (1999) argue that by categorizing landscapes as natural and human-influenced, the effect is the creation of a false-dichotomy since humans have greatly modified ecosystems for millennia. Secondly, the concept implies that human presence is always harmful. In some cases the effect of human presence is less detrimental and sometimes beneficial (Bishop et al., 1981). For example, human disturbance has resulted in increased food availability and increases in primate population size and density of *Macaca fascicularis* in two sites on the island of Bali, Indonesia (Wheatley & Harya Putra, 1994a, 1994b). Cormier (1999) suggests that certain indigenous cultural practices of the Guajá Indians in Brazil, such as sustainable hunting practices and the provision of refuges from habitat destruction, actually benefit primate conservation. Furthermore, in some areas (e.g., Amazonia and Southeast Asia) traditional swidden agriculture, like small-scale disturbances in the forest, has been shown to enhance the overall biodiversity of the area (Spencer, 1966; Wharton, 1968; Park, 1992; Sponsel, 1992; McNeely, 1994; Sponsel et al., 1996).

On the other hand, human-induced changes in the environment, such as the destruction of key aspects of habitat (e.g., food sources and sleeping trees) or the conversion of usable habitat to other types (e.g., agricultural areas and grasslands), can result in serious damage to primate populations (Johns, 1986; Johns & Skorupa, 1987; Skorupa, 1988; Johns, 1991; Struhsaker, 1997; Rosenbaum et al., 1998; van Schaik et al., 2001; Paciulli, 2004). The impact of anthropogenic habitat alteration on primate populations ultimately depends on the nature and scale of the disturbance and the extent of the primates' ecological and behavioral flexibility in response to changes (Wilson & Wilson, 1975; Marsh & Wilson, 1981; Marsh et al., 1987; Skorupa, 1988).

Marsh et al. (1987) indicate that there are at least six categories of human-induced disturbance to forest habitat: (1) the removal of selected plant products (e.g., rattan), the effect of which depends on the importance of those plant products to the diets of primate species in question, (2) clearance or damage to the forest understorey, (3) changes in the water regime, (4) shifting cultivation, which creates a mosaic of small-holder farmland and secondary forest, (5) commercial selective logging, and (6) large-scale clearance for plantations or ranching. Such categorizations, however, serve only as heuristic devices, since habitat alteration often originates from the interaction of a number of these practices. For example, although in most cases the trees of greatest commercial value are typically not those used as food trees by resident primate species, many non-timber trees, and potential food sources, are destroyed during the logging process (Wilson & Johns, 1982; Johns, 1986). Strangler figs (*Ficus* spp.), which often serve as important resources for primates as well as other forest animals, particularly during periods of food scarcity, grow preferentially on large trees and therefore may be particularly susceptible to damage (Leighton & Leighton, 1983; Terborgh,1986). Their loss may significantly contribute to a reduction in primate abundance in those disturbed areas (Wilson & Johns, 1982). On the other hand, low intensive selective logging (e.g., hand-logging by local people) can result in the emergence of new vegetation (Wilson & Wilson, 1975). Secondary forests can often support higher densities of food resources than mature forests due to the abundant and diverse fruit supply in the understorey[3] (Chivers, 1974; Corlett, 1995), and may therefore support higher primate densities (Oates et al., 1990; Thomas, 1991; Fimbel, 1994; Plumptre & Reynolds, 1994). This suggests that selective logging may not always lead to a decrease in primate populations.

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[3] Chivers (1980) argues, however, that actual food availability is greater in less disturbed habitats because many of the pioneer species that recolonize recently disturbed (i.e., through logging) forest are not species used by most mammals and birds.

Nonetheless, because small-scale human forest use tends to occur as an on-going process over long periods of time, it is still an important source of habitat alteration and can potentially be just as devastating (Struhsaker, 1997).

In Indonesia, like most of Southeast Asia, the two major activities that alter and/or destroy primate habitat are shifting cultivation and logging of tropical forest hardwood (Wilson & Wilson, 1975; MacKinnon 1986, 1987). Concurrent with continued conversion of forest habitat to agricultural areas is an increasingly predominant form of human disturbance/influence: the encroachment of human settlements along the edge of protected forest habitats. Such encroachments can be problematic for wildlife for at least two reasons. First, encroachment by agriculture results in the creation of new ecological edges, which can alter the microclimate (especially light, temperature, and humidity) and encourage a shift in the composition of wildlife and plant species, thus changing the biodiversity of the area (Janzen, 1986; Lovejoy et al., 1986; Struhsaker, 1997). Secondly, human encroachment upon the forest edge brings wildlife in closer proximity to humans. Human-nonhuman primate proximity, however, is by no means a recent phenomenon, but rather exhibits a long history (Sponsel et al., 2002). For example, rhesus monkeys (*Macaca mulatta*) "have lived in close ecological contact with man for centuries and persistence in this commensal relationship in villages, towns, and roadsides represents a natural relationship" (Southwick et al., 1965: 158). Richard et al. (1989), by analyzing the feeding/foraging patterns of members of the genus *Macaca*, found that certain macaques have the ability to persist and even prosper in close proximity to human settlements. They categorized species of *Macaca* as "weed" and "non-weed" based on their differences in frequency and success in exploiting human resources. The authors argue that the ability of macaques to prosper in close proximity to humans should be recognized as an integral and interesting part of their ecological strategy.

Human proximity has been shown to have important, and potentially negative, demographic and socioecological consequences for nonhuman primates (Bishop et al., 1981). For example, the disruption of habitat by human encroachment may compress animals into smaller home ranges, thereby increasing local density (Bishop et al., 1981). Human-nonhuman primate proximity can also result in increased likelihood of bi-directional disease transmission (Fa, 1991; Engel-Jones, 2001). In addition, and most relevant for this project, proximity may increase the likelihood of conflict between human and nonhuman primates, particularly in the form of hunting and crop raiding. Although habitat destruction is recognized as the most significant threat to wild primate populations, depending on the region and the species under consideration, hunting also poses a serious threat to primate populations (Mittermeier, 1987; Mittermeier & Cheney, 1987; Peres, 2000). Primates are hunted by humans for a number of reasons including: for medicinal purposes, for food, to dispel evil omens, to use as bait for other animals, to use skins or other body parts for ornamentation, to use as pets, to use them as “sport” hunting animals, and because they are agricultural pests (Mittermeier, 1987).

High rates of human population growth in areas of the world where nonhuman primates are indigenous continues to lead to the expansion of agricultural areas, often encroaching upon wildlife habitats, thus increasing the likelihood of human-wildlife conflict. Some primate species can adapt to such alterations in their environment by incorporating agricultural areas into their ecological repertoire. Because these animals frequently raid agricultural areas, they are subsequently deemed “pests” by human residents (Else, 1991). The most common (and successful) “pest” species among the Old World primates include members from the genera

Macaca, *Papio,* and *Cercopithecus* (Brennan et al., 1985; Else, 1991; Newmark et al., 1993; Strum, 1994; Hill, 1997; Saj et al., 1999). Their success is largely attributed to their possession of a complex social organization, their ability to utilize both terrestrial and arboreal habitats, and their reliance on non-specialized and omnivorous diets (Forthman-Quick, 1986; Else, 1991). The extent to which crop raiding is a problem depends on the location of crops in relation to wildlife habitats and the distance of the crops from such habitats, the types of crops grown, and people's ability to protect their crops from invading animals (Hill, 1997). Because crop raiding poses a serious challenge to the future conservation of many primate species (Strum 1994) and conservation inherently involves the values and actions of humans, it is critical that research address both sides of the conflict; that is, examining crop raiding as part of a primate's ecological strategy and how this strategy affects the livelihoods of local farmers.

Human-nonhuman primate conflict and competition can also emerge as a result of overlapping uses of forest resources. The conservation significance of overlapping resource use is contingent upon the importance of the forest product for the diets of the primate species and for the livelihoods of the human users. At the Tana River Reserve in Kenya, Kinnaird (1992) found that the palm, *Phoenix reclinata*, is both heavily exploited by people of the Tana River District and provides an important food source for the endangered Tana River crested mangabey. Thus, in this case, from a conservation perspective, it is critical that human use be monitored so that the palm can persist for future use by both the mangabeys and human residents. In Lore Lindu National Park, residents of boundary villages collect a number of forest products including rattan, timber, fuelwood, animals (mostly wild pigs for food), honey, medicinal plants, and butterflies (Schweithelm et al., 1992). Where nonhuman primates share forest habitat with humans, such as in Lore Lindu National Park, an important question to examine is whether

Tonkean macaques and villagers have competing uses for forest resources. If these resources represent important food resources for the macaques, it then becomes critical to know if human use will influence the long-term persistence of the resources and thereby have a potentially negative impact on both the people and the macaques.

The National Park concept is, historically, a western-based idea with the goal of strict nature protection (Hough, 1988; McNeely, 1989; Stevens, 1997). The last century, however, has witnessed the transformation of this concept to a major global phenomenon (Stevens, 1997). Yellowstone National Park serves as the model, the world standard, in which settlement and both subsistence and commercial uses of the natural resources are prohibited (Stevens, 1997; Neumann, 1998). Beginning in the 1980s and increasingly so in the last decade, the international conservation movement has begun to place less and less emphasis on the traditional model of human exclusion, by recognizing that successful management must include the cooperation and support of local people (Brandon & Wells, 1992; Vandergeest, 1996; Stevens, 1997). The evolution of the concept of "protected areas" is evident in the redefinition by the IUCN of protected area categories from 1978 to 1994. The 1994 classification scheme exemplifies a gradation of human inclusion, whereby protected areas vary in the degree to which they recognize resident peoples' settlement and subsistence practices and their involvement in natural resource management. Biosphere Reserves represent a good example of this gradation of human inclusion. Recognized by UNESCO's Man and the Biosphere Program, these zone-based protected areas often encompass a National Park or strict nature reserve as their core area, buffered by surrounding controlled areas where some forms of utilization are allowed (Hough, 1988; Stevens, 1997).

Recent scholarship on the subject of protected areas, however, remains contentious. The points of contention ultimately stem from varying perspectives on how nature (and similar concepts such as wilderness and biodiversity) should be defined and the place of humans in nature. Those who espouse a biocentric[4] approach envision a wilderness that is and should be separate from humans (Graber, 1995). The biocentric perspective also hinges on an aesthetic and spiritual argument for protecting nature (e.g., Soulé, 1995; Terborgh, 1999; Oates, 1999). Proponents of this perspective have issued a number of recent critiques that contend that conservation efforts are failing, arguing for a return to a more authoritarian approach to conservation (e.g., Kramer et al., 1997; Brandon et al., 1998; Oates, 1999; Terborgh, 1999). The main argument of these critiques is that people-based conservation efforts focus too much on social concerns to the neglect of nature and that often efforts to incorporate human concerns actually exacerbate threats to conservation and promote biodiversity loss. Those who espouse a more anthropocentric (i.e., people-based) approach challenge the notion of an unspoiled wilderness and argue that wilderness encompasses an enormous amount of human history, for humans have long played an active role in altering and maintaining what it is that we call "nature" (Spencer, 1966; Williams, 1980; Botkin, 1990; Adams & McShane, 1992; Cronon, 1995). Proponents of this view contend that nature protection is not just about nature, it is a social and political process and social justice is central to achieving conservation (Alcorn, 1993; Brechin et al., 2002; Alcorn, forthcoming). Within the context of protected area conservation, an important question becomes: How are local human livelihoods affected by the designation of protected "natural" areas? Neumann (1998) contends that many protected areas have been created out of lands with long histories of human occupancy and use, rather than being areas of

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[4] Although I present the perspectives as a dichotomy (i.e., biocentric versus anthropocentric), I should point out though that in reality peoples' viewpoints tend to fall more along a continuum rather than in "either or" categories.

"unspoiled wilderness." As a result, the establishment of National Parks and other protected areas is often viewed as an act that criminalizes customary land and natural resources uses for many communities across Africa (Ghimire, 1994; Stevens, 1997; Neumann, 1998) and Southeast Asia (Ghimire, 1994; Vandergeest 1996).

Lore Lindu National Park represents an example of a UNESCO Biosphere Reserve in which some land use activities are allowed in the buffer zone[5] areas. Lore Lindu is surrounded by 117 villages, with approximately 120,000 residents, half of whom are migrants who have arrived since 1980 due to the transmigration program[6] (TNC, 2001). In a number of the village areas around the park, however, no such buffer zones exist, nor do local people even know that they are supposed to exist (Riley et al., 2000). As a result, a major problem for the park, as perceived by the state conservation agency and its international NGO counterpart, is the increasing human settlement on adjacent lands and unauthorized harvesting of resources within the park. For example, recent reports indicate that the Lake Lindu enclave area is experiencing inward migration and concomitantly, additional clearing for agriculture, and timber removal, thus leaving only a 4-km band of forest between the edge of the park and the expanding agricultural areas (Smithers, 2000). As the human population increases in this area and the demand for resources grows, the frequency and intensity of negative feelings held by local people toward the protected area are likely to increase (e.g., Newmark et al., 1993). Currently, many villagers resent the presence of the park due to its boundaries cutting through previously established coffee gardens and reducing the amount of land available to them for expansion of dryland farming (Schweithelm et al., 1992). This potential for conflict is exacerbated by the fact

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[5] A buffer zone is a strip of forest that surrounds a core area of forest (e.g., strict nature reserve) where some land use activities are allowed.

[6] In 1952, a 35-yr Transmigration plan was implemented with the primary objective of improving the standard of living of the Indonesian people by moving them from the overpopulated Java to the Outer islands (Mantra 1985).

that wildlife within the forests, such as the Tonkean macaques, do not recognize park boundaries and are attracted to adjacent agricultural areas (Riley et al., 2000). Human-monkey conflict arising from crop raiding may also negatively impact the conservation norms of the local communities who live in close proximity to forests. For example, in many parts in Africa and Asia, nonhuman primates are considered a threat to crops and thus, to human livelihoods, rather than a resource to be conserved (Hill, 1997; Naughton-Treves, 1997; Siex & Struhsaker, 1999; Riley et al., 2000).

In an attempt to mitigate the conflict between local residents and protected areas, and to realize the goal of effective conservation management, conservationists are increasingly recognizing that protected areas need to be managed within a broader ecological framework that includes the cooperation and support of local people (Brandon & Wells, 1992; Wells & McShane, 2004). Anthropologists, and other social scientists, have contributed to this movement with their insight into patterns of human behavior; for example, environmental ideologies and decision-making that encourage or impede conservation efforts (Orlove & Brush, 1996; Mascia et al., 2003). Research examining local attitudes towards conservation has shown that the people who must live adjacent to protected areas often do not share the same conservation values and attitudes as western conservationists (Boonzaier, 1996). For example, Kottak & Costa (1993) contend that in Madagascar, the economic value of forest (e.g., watershed protection) represents a much more meaningful incentive against forest degradation than do global goals like “preserving biodiversity” or lemur conservation. What we can expect, perhaps, is working towards a convergence of values (Harcourt et al., 1986; Weber, 1987). For example, differing conservation attitudes between conservationists or park managers and local populations may be due to a disagreement in the *process* of conservation (e.g., specific management actions) rather than the in the concept of conservation (Infield, 1988).

Anthropological primatology has also contributed to this movement with a new approach, ethnoprimatology, which addresses the ecological and cultural interconnections between human and nonhuman primates, and the implications these interconnections have for conservation (Sponsel, 1997; Fuentes & Wolfe, 2002). A key feature of this approach is abandoning the idea of a pristine environment and instead, envisioning humans and nonhuman primates as members of a dynamic ecosystem. Furthermore, it moves beyond the traditional boundaries of the science of primatology, ethnography, and conservation, and treats these fields as a unified area of investigation. For example, Sicotte & Uwengeli (2002), by examining how Rwandans envision the forest and gorillas that live there, found that although gorillas do not figure prominently in Rwandan folklore, they are recognized as closely related to humans and therefore are not sought after for bushmeat. The authors suggest that this information is critical for the development of conservation programs that are better suited to the people of Rwanda.

Research setting

This research was conducted in the villages and surrounding forest of Tomado and Anca in the Lake Lindu enclave in Lore Lindu National Park in Central Sulawesi, Indonesia. The Lake Lindu area is one of two valley enclaves that are allowed to exist within the National Park because it is a major rice growing area and has long established settlements. Lore Lindu National Park was established in 1993 from two existing reserves; the Lore Kalamanta Nature Reserve and the Lake Lindu Recreation and Protection Forest (TNC, 2001). Lore Lindu is currently one of the largest National Parks in Sulawesi, comprising a total area of 217,982 ha, and has been declared a Man and the Biosphere Reserve by UNESCO (TNC, 2001).

The park's flora is generally classified into two major vegetation types based on altitudinal distribution, with lowland forest (below 1000m) covering less than 10% of the park and montane forest (above 1000m) comprising the remaining 90%[7] (Wirawan, 1981). Annual rainfall in the park averages between 2000-3000mm, which is evenly distributed over the year except for a slight increase between November and April (Watling & Mulyana, 1981; Supriatna et al., 1992). Lore Lindu National Park provides habitat for a majority of Sulawesi's endemic mammals, including the mountain anoa (*Bubalus quarlesi*), the babirusa (*Babyrousa babyrussa*), two species of the marsupial cuscus (*Phalangar ursinus*, *P. celebensis*), three species of tarsier (*Tarsius spectrum*, *T. dianae*, *T. pumilus*), and one of the seven endemic macaques, *Macaca tonkeana*.

Macaca tonkeana, which occurs only in Central Sulawesi, is among the least-known species on the island with regard to socioecology and conservation status. Over a decade ago, Whitten et al. (1987) categorized *M. tonkeana* as the most common and least threatened Sulawesi macaque. MacKinnon (1986) suggests, however, that although large reserves have been established in Central Sulawesi (e.g., Morowali and Lore Lindu), much of the area (i.e., montane forest) within their boundaries may not be suitable habitat for *M. tonkeana*. The Sulawesi Tonkean macaque is currently listed as "Lower Risk/Near Threatened" (IUCN, 2004) with a proposed total population estimate of 150,000 individuals (Bynum et al. 1999). It is likely, however, that this figure may require revision because crop raiding by macaques appears to be a growing problem in Sulawesi (Supriatna et al., 1992; Riley et al., 2000), with groups living in proximity to human habitation raiding gardens and agricultural land on a regular basis. Secondly, there is evidence of increasing hunting pressure on macaques in Central Sulawesi for

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[7] Whitten et al. (2002) propose a new designation of lowland and hill forest representing 0-1500m, lower montane forest as 1500-2400m, upper montane forest as 2400-3000m, and subalpine forest as 3000m +.

local consumption and for meat markets in Manado, North Sulawesi (Lee, 1999). Reports of estimated population density of *M. tonkeana* vary considerably: Alvard (1999) reports densities of only 2.2 individuals/km^2 whereas Supriatna et al. (1992) report a range between 19.2 to 23.3 animals/km^2.

The northwest part of the National Park, where the Lindu valley is situated, is primarily occupied by the Kaili people (TNC, 2001). In the Lindu valley, the Dutch conquest of the Kaili hinterland, which began in 1902, resulted in the concentration of hill farmers into three settlements (i.e., Anca, Tomado, and Langko) along the lakeside (Acciaioli, 1989; Li, 2000). The *To Lindu*, indigenous to the Lindu valley, are members of the Kaili ethnic group which is further divided into seven distinct groups on the basis of dialect, with the Lindu form referred to as Kaili Tado' (Acciaioli, 1989; TNC, 2001). At the time of the Dutch conquest, the *To Lindu* population subsisted primarily on *ladang*[8] agriculture, consisting of maize, tubers and other dry crops, but they also practiced wet-rice agriculture, as evidenced by the remains of previously worked wet-rice fields found by the Dutch (Acciaioli, 1989).

Although the Lindu valley remained a relatively isolated enclave throughout the colonial era and post-independence, recent immigration has included other Kaili people from Kulawi, as well as Bugis people from South Sulawesi, who are attracted to the area for wet-rice agriculture, perceived available land for the planting of important cash crops, such as coffee and cacao, and the development of a fishing industry at the 3,000 ha lake (Schweithelm et al., 1992). The predominant form of agriculture in Lindu is currently wet-rice agriculture (*sawah*), practiced by

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[8] Shifting cultivation

both indigenous Lindu and migrants, but tree cash crops, such as coffee and cacao, have also become an important part of the Lindu economy.

Dissertation overview

During the summer of 2000 I conducted a preliminary investigation of factors affecting the conservation status of *M. tonkeana* in Lore Lindu National Park (Riley et al., 2000). Based on this research, I found that there are three major ecological ramifications of human settlements bordering on the habitat of *M. tonkeana* in the National Park: (1) the alteration of forest, such as cutting paths for rattan and firewood collection, and the disturbance associated with their collection, (2) the development of agricultural areas (either in semi-cleared forest patches for coffee crops or total clearing for crops such as maize, cacao, and bananas) that encroach upon the forest edge and the disturbance associated with this, such as edge effects, and (3) the increased likelihood of human-nonhuman primate interactions, such as crop-raiding and hunting.

In this dissertation, I built upon this preliminary research and Schweithelm et al.'s (1992) work on land uses and the socioeconomic conditions of villagers throughout the National Park, by examining the interface of human ecology, primate ecology, and conservation in the Lake Lindu enclave of Lore Lindu National Park. I had two overall research goals. The first goal was to examine how Sulawesi Tonkean macaques respond to anthropogenic habitat alteration in terms of their (1) feeding/foraging patterns, (2) diet composition, (3) activity patterns, and (4) ranging patterns. The second goal was to assess how particular aspects of local human ecology affect the ability of *M. tonkeana* to persist in Lore Lindu National Park. I accomplished this latter goal by examining (1) the conservation implications of overlapping use of both anthropogenic (i.e., crops) and forest resources between villagers and Tonkean macaques, and

(2) how human perceptions of the environment (i.e., forests, protected areas, and wildlife) affect the conservation of Tonkean macaques in the Lindu valley.

Anthropogenic habitat alteration, which often results in lower quality habitat characterized by a diminished food supply (Struhsaker, 1997), can produce "resource-scarce" ecological conditions to which primates often respond by adjusting their behavior. The first two chapters address this concern by examining the behavioral responses of Sulawesi Tonkean macaques to human habitat alteration. These chapters are based on the premise that intraspecific comparisons of diet, activity patterns, ranging patterns, and habitat use of groups living in different levels of disturbance can elucidate the behavioral and ecological flexibility of Tonkean macaques in the face of change. The first manuscript (chapter 2) focuses on how these primates respond in terms of their diet and activity patterns, and the second manuscript (chapter 3) examines ranging patterns and habitat use in relation to habitat quality. Anthropogenic habitat alteration was defined as the clearing of forest for agriculture and small-scale forest product collection. I studied two macaque groups whose habitats differed in levels of human alteration. The first group (Anca) occupied heavily-altered forest, characterized by frequent use by villagers (e.g., tree felling for livelihood needs) and conversion of forest to agricultural and agroforestry areas. The second group (CH) occupied minimally-altered forest (i.e., no agricultural areas, except one coffee agroforest garden on the southwestern edge of the group's range, yet frequent collection of rattan) inside the boundary of the National Park. Due to differences in habitat alteration between the two groups' habitats, I expected concomitant differences in habitat quality. I defined habitat quality in terms of the abundance, diversity, productivity, and distribution of potential food resources, and analyzed these to demonstrate that the human alteration of the Anca group's habitat did indeed result in lower quality habitat.

For the first manuscript, I collected data on forest structure, composition, and fruit availability to test the following predictions: given that human habitat disturbance often involves the removal of large trees for timber and/or for space to plant crops, I expected (1) the minimally-altered habitat to have a greater percentage of mid-canopy (i.e., 16-29 cm DBH) and canopy sized (i.e., > 30cm DBH) trees than the heavily-altered habitat, (2) mean DBH to be greater in the minimally-altered habitat than in the heavily-altered habitat, and (3) fruit production to be greater in the minimally-altered habitat than in the heavily-altered habitat due to a greater occurrence of canopy and mid-canopy sized trees. I collected data on the diet and activity patterns of the two macaque groups to test the following predictions: the group living in heavily-altered habitat was expected to (1) consume more alternative food items, (2) show less dietary diversity, and (2) spend more time foraging, feeding, and moving, and less time resting and socializing, than the group in minimally-altered habitat, due to differences in habitat quality that result from anthropogenic habitat alteration.

For the second manuscript (chapter 3), I collected data on movement patterns (i.e., daily path length) and the use of space (i.e., microhabitat use, forest strata use, home range use) to test the following predictions: (1) time spent in different forest strata was expected to be related to differences in habitat quality, with the group in heavily-altered habitat expected to spend more time on the ground (i.e., because there are fewer trees available for foraging and travel), (2) the groups were expected to spend more time in continuous forest areas (i.e., because these areas tend to have greater fruit abundance due to a higher occurrence of mid-canopy and canopy-sized trees), than more altered microhabitats (e.g., agroforested areas), (3) daily path length and home range size were expected to be greater for the group occupying heavily-altered habitat, and (4) intensity of range use was expected to differ between groups, with the group living in heavily-altered habitat expected to use certain quadrats more intensely than others, due to reduced abundance of food resources and a more patchy distribution of those resources across their range.

The last two manuscripts (Chapters 4 & 5) address the question of how local human ecology affects the conservation of *Macaca tonkeana*. I broadly define human ecology as the ways individuals interact, both actively and conceptually, with their environment. The third manuscript (chapter 4) addresses the active realm by investigating overlapping resource use between villagers and Tonkean macaques in the Lindu enclave in Lore Lindu National Park. The premise of this chapter is that human-nonhuman primate sympatry need not be viewed as an "unnatural" situation, but rather as an interesting example of community ecology that has important implications for conservation. For this manuscript, "resource use" includes the utilization and exploitation of both forest resources and anthropogenic resources (i.e., cultivated foods). I determined which forest resources are important for both macaques and humans and examined how the manner of human exploitation of these resources affects the potential use by macaques. I address both "sides" of the overlapping use of anthropogenic foods by (1) examining farmers' assessments of the impact of crop raiding on their livelihoods, and (2) quantitatively measuring macaque crop raiding on cacao tree crops (*Theobroma cacao*). The results from this research are discussed with regard to the implications of overlapping resource use for the conservation of *M. tonkeana*.

The final manuscript (chapter 5) addresses the conceptual realm of human ecology by examining villagers' perceptions of the National Park and conservation, and how the Tonkean macaque figures into local folklore, in order to assess how conceptualizations of the environment contribute to or impede conservation in the Lindu valley of Lore Lindu National Park.

Overview of methods

Assessment of habitat quality

I collected data on forest structure, composition, and phenology to assess differences in habitat quality between the ranges of the two macaque groups. Several measures were used to determine habitat quality: species richness, diameter-at-breast height (DBH), tree basal area, the diversity and spatial distribution of potential food resources, and forest fruit abundance. I established a total of 40 vegetation plots, each 25m x 25m, per habitat. In each plot, I identified and measured every tree = 10 cm DBH. Because members of *Ficus* spp. have been identified as important food resources for other Sulawesi macaques (Kohlhaas, 1993; Lee, 1997; O'Brien & Kinnaird, 1997), I recorded the presence of all fig species in the vegetation plots. Each tree was assigned to a size class according to the following categories (Lee, 1997; Whitten et al., 2002): DBH ≤ 15cm = understorey (< 20m height); DBH 16-29 cm = mid-canopy (20-30m height); DBH ≥ 30cm = canopy (> 30m height). A total of 1153 trees representing 175 species, and 763 trees representing 163 species, were sampled in the CH and Anca groups' habitats, respectively.

From these 40 plots I then selected 10 to monitor the phenological phases of all trees = 20 cm DBH, all fig species, and any other tree species known to be a Sulawesi macaque food item (based on preliminary observations, and other studies of Sulawesi macaques) from each habitat. The phenological state of each tagged tree was estimated once a month on predetermined dates via visual examination with binoculars. Percentages of new leaves, flowering buds, flowers, unripe fruit, and ripe fruit were estimated (i.e., proportion of the total canopy covered by the item) and assigned an abundance score from 0-4, where 0 = 0% of the canopy, 1 = 1-25%, 2 = 26-50%, 3 = 51-75%, and 4 = 76-100%.

Nonhuman primate behavioral observations

Because this project was the first to study the ecology and behavior of *M. tonkeana* at the chosen field site, I spent a number of months (Anca: 7 months, CH: 5 months, Kalora: 8 months), prior to the start of systematic data collection, habituating the first two groups to the point of tolerating human presence at a distance of less than 10 m. Because I was never able to fully habituate the Kalora group and systematic behavioral observations on this group are therefore incomplete, I only include data from ad libitum observations on this group in the manuscripts. Following habituation, the two groups (Anca and CH) were followed from 0600-1800 hours on 3 consecutive days once a month for 15 months, between January 2003 and April 2004. Following Kinnaird (1990), every half hour, 10 minutes were spent taking a scan sample (Martin & Bateson, 1993) of the group, recording the following information for each individual located: (1) age/sex (5 classes: adult male, adult female, large juveniles, small juveniles, and infants), (2) food item if eating (and species if known): young leaves, mature leaves, fruit (ripe or unripe), stems, shoots and sprouts, seeds, flowers, insects, and crops (type & part), (3) the first activity sustained for at least 5 seconds, (4) location in the forest strata (categories: 0m (on ground), >0-2m, >2-12m, >12-20m, and >20m), and (5) microhabitat type. Microhabitat types were defined as: (1) continuous forest: forest bounded on =1 side by agroforestry/agricultural areas, (2) broken forest: forest areas separated from continuous forest on =2 sides by agricultural areas, and (3) forest garden: agricultural areas present within the forest. Recorded activities included *moving*, *foraging*, *feeding*, *resting*, and *social/sexual*. A total of 747 scans, over 373.5 hours across 45 days were collected for the Anca group. For the CH group, 473 scans were collected during 236.5 hours across 36 days.

Immediately following a 10-min scan sample, I estimated and plotted the center-of-mass of the study group at half-hour intervals on the map of the group's habitat. I mapped movement on 41 days for the Anca group, and 26 days for the CH group. Daily path length (DPL) was calculated by summing the straight-line distances between half-hour center-of-mass locations during a single day (Altmann & Altmann, 1970). Overall home range was estimated by drawing a line around the outermost sightings of the group (including ad libitum observations) and counting the number of quadrats within the line (Altmann & Altmann, 1970; Lee, 1997). I also calculated annual home range by summing the number of unique quadrats entered at 12 months. To investigate the intensity of home range use, I tabulated the number of times each group entered each quadrat within their range over the study period.

Quantitative assessment of crop raiding

I monitored 11 cacao gardens for crop damage caused by the macaques, forest mice (Family Muridae), and forest squirrels (Family Sciuridae) from Dec 2002 – August 2003. In each cacao garden, each cacao tree was counted, assigned a number, and the shade management system used in the garden was noted (Codes: 1 = Mix of thinned primary/older secondary forest with planted shade trees (*Erythrina* spp., *Musa* spp.), 2 = Planted shade trees with occasional remnant forest species, 3 = No shade, 4 = Little to no shade (a few remnant forest species present)). Every two weeks each garden was surveyed and the following information was recorded for each tree in the garden: the number of fruits remaining on the tree, and the number of fruits eaten by macaques, mice, and squirrels based on the remains of consumed cacao fruits. To determine whether crop raiding is related to patterns of forest fruit availability, I collected phenological data from 10 vegetation plots (25 X 25 m) that were established within the home range of the Kalora group (a group known to raid cacao gardens), using the method described above.

Ethnography

I collected information on human forest resource use through personal observation and formal interviews with villagers (*n* = 45) from Anca and Tomado. Respondents for the formal interviews were selected using a chain-referral approach (Bernard, 1995). The interviews included freelisting exercises, for which I asked respondents to list all forest resources and tree species known to them and the purpose/function of those resources.

I conducted interviews with 11 cacao farmers in which I asked them to assess the frequency of crop raiding (i.e., never, occasionally, frequently, very frequently), and how crop-raiding affected their livelihoods. I also asked respondents from the human product forest use interviews to list all animals that raid crops.

I collected information on perceptions of the forest, the National Park, and conservation through informal and formal interviews with the set of respondents mentioned above (*n* = 45). The formal interviews included the following questions: (1) what is the purpose/function of Lore Lindu National Park, (2) what are the benefits of the National Park, (3) what are the negative outcomes of the National Park, (4) what are the threats towards the National Park, and, (5) what are the benefits of conservation. Although these questions were treated as freelists on a particular domain of knowledge (e.g., purpose of a National Park), respondents elaborated on their responses as they felt necessary. I then coded these open-ended responses into practical categories (Fleisher & Harrington, 1998). For example, the response, “protect everything in the forest so that it does not go extinct,” to the first freelist question was coded as “nature protection.”

Informal discussions with villagers upon my arrival in Lindu revealed that *To Lindu* folk ecology includes stories about human-macaque interactions. Respondents of the formal interviews were therefore asked to recount folklore they knew regarding the relationship between humans and macaques, human-macaque interactions, or human-macaque conflict. In order to fully document this folklore, I conducted informal interviews with individuals who were identified by other villagers as ones who knew the stories.

CHAPTER 2

FLEXIBILITY IN DIET AND ACTIVITY PATTERNS OF THE SULAWESI TONKEAN MACAQUE (*Macaca tonkeana*) IN RESPONSE TO ANTHROPOGENIC HABITAT ALTERATION[1]

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[1] Riley, E.P. To be submitted to *International Journal of Primatology*.

ABSTRACT

The objective of this study was to examine how Sulawesi Tonkean macaques (*Macaca tonkeana*) respond in terms of their diet and activity patterns to anthropogenic habitat alteration in Lore Lindu National Park, Sulawesi, Indonesia. Anthropogenic habitat alteration was defined as the clearing of forest for agriculture and small-scale forest product collection. The diet and activity of two groups (CH and Anca), occupying habitats with different levels of alteration, were quantified using scan sampling. Tree abundance, key food species density, and fruit production were found to be greater in the minimally-altered habitat (CH), substantiating the characterization of this group's habitat as higher quality. For the group in the heavily-altered habitat (Anca), alternative foods accounted for a significantly greater proportion of the diet. Dietary diversity was significantly lower in the Anca group, with 52% of their diet comprised of only one resource, the palm fruits from *Arenga pinnata*. The activity patterns of the Anca group (more time foraging, less time moving, and more time resting than the CH group) reflect the lower resource availability in their habitat and their reliance on more alternative food items, coupled with their extremely small group size (6-9 animals). This group may be at the optimal size in which foraging efficiency is maximized for the habitat, a response, in conjunction with dietary and behavioral flexibility, to alteration of their habitat. These results are contextualized with respect to the conservation value of human-modified landscapes.

Key words: flexibility; habitat quality; human habitat alteration; diet; activity patterns; Sulawesi macaque

INTRODUCTION

Throughout the tropics, development activities, logging, and agricultural expansion have resulted in the conversion of previously continuous forests to landscape mosaics of forest fragments, secondary vegetation, and agricultural areas (Marsh et al., 1987; Mittermeier & Cheney, 1987; Harris & Silva-Lopez, 1992). Nonhuman primates that inhabit such mosaics face a number of ecological constraints, including lower tree species richness, diversity, and density (Turner, 1996; Lee, 1997; Struhsaker, 1997), reduced food availability (Johns, 1988, 1991; Struhsaker, 1997), restricted home ranges (Menon & Poirier, 1996), and increased competition (Dittus, 1977). These ecological constraints can, in turn, impinge upon diet, reproduction rates, mortality rates, and thus, ultimately, upon the survival of nonhuman primates (Menon & Poirier, 1996).

The impact of anthropogenic habitat alteration on nonhuman primate populations, however, depends on the nature and scale of the disturbance, the time since modification took place, and the extent of the primates' ecological and behavioral flexibility in response to changes, which can vary among primate taxa (Wilson & Wilson, 1975; Marsh & Wilson, 1981; Johns & Skorupa, 1987; Marsh et al., 1987; Skorupa, 1988; Singh & Vinathe, 1990; Pearl, 1992). Logging, for example, although typically large in scale, has not been uniformly associated with decreases in primate populations (Wilson & Wilson, 1975; Fimbel, 1994; Plumptre & Reynolds, 1994). It should be acknowledged, however, that many non-timber trees and potential food sources, however, are destroyed during the logging process (Wilson & Johns, 1982; Johns 1986, 1988; Okuda et al., 2003). Strangler figs (*Ficus* spp.), which often serve as important resources for primates as well as other forest animals, particularly during periods of food scarcity, grow preferentially on large trees and therefore may be particularly susceptible to damage (Leighton & Leighton, 1983; Terborgh, 1986). In addition, small-scale human forest use, because it tends to occur as an on-going process over long periods of time, is also an important source of habitat alteration and can potentially be just as devastating as large scale forms of disturbance (Struhsaker, 1997).

The genus *Macaca*, because of its extensive geographic range and occurrence in a diversity of habitats (Albrecht, 1978; Fooden, 1980; Fa, 1989), is believed to be highly tolerant to changes in their habitat (Richard et al., 1989). For example, some macaques can exploit new sources of food in the forest (Berenstain, 1986; Nakagawa, 1989; Singh et al., 2001), while others have adapted to the expansion of agricultural areas by incorporating these areas into their ecological repertoire (Wheatley, 1980; Wada, 1984; Eudey, 1986; Richard et al., 1989; Supriatna et al., 1992; Hsu & Agoramoorthy, 1997; Riley et al., 2000; Sprague, 2002). Agreement on whether such high levels of tolerance and adaptability to habitat disturbance should be generalized to all members of the genus remains equivocal, however, as a number of the macaque species remain red-listed as ‘Data Deficient’ (*M. ochreata*), ‘Endangered’ (*M. fuscata* ssp. *yakui*, *M. maurus*, *M. nigra*, *M. silenus*) or ‘Critically Endangered’ (*M. pagensis, M. pagensis* ssp. *pagensis*, *M. pagensis* ssp. *siberu*) (IUCN, 2004). This lack of agreement results primarily from a void of information on the behavior and ecology of wild populations of a number of the macaque species. For example, although the Sulawesi macaques have been observed in a variety of habitats, most of these studies have been short in duration (e.g., Watanabe & Brotoisworo, 1982, 1985; Sugardjito et al., 1989; Supriatna et al., 1992; Bynum, 1994). Of the seven endemic Sulawesi macaques (Fooden, 1969), only two have been the subjects of long-term ecological and behavioral research (*M. nigra*: Lee, 1997; O’Brien & Kinnaird, 1997; *M. nigrescens*: Kohlhaas, 1993). With such limited data, our understanding of

Sulawesi macaques' tolerance of habitat loss and disturbance, and their ability to persist in resulting marginal habitats, remain unclear (Lee, 1997).

Intraspecific comparisons of diet composition and the proportion of time spent in different activities of groups living in habitats with different levels of disturbance represent one approach to investigating how nonhuman primates respond to human habitat alteration, and thus the extent of their behavioral and ecological flexibility in the face of change (Kinnaird, 1990; Singh & Vinathe, 1990; Wieczkowski, 2003). Diet composition of nonhuman primates is constrained primarily by resource availability. In tropical forests, resource availability is often highly variable, marked by a large peak in supply followed by a prolonged period of resource scarcity (Leighton & Leighton, 1983). In general, the majority of frugivores in such areas will either migrate or shift their diets during such periods of food scarcity (Gautier-Hion, 1980; Leighton & Leighton, 1983; Berenstain, 1986; Terborgh, 1986; DaSilva, 1994; Doran, 1997; Kaplin & Moermond, 2000). Habitat alteration, which can result in a diminished food supply, may also produce similar "resource-scarce" ecological conditions to which primates must respond. For example, Singh et al. (2001) found that lion tailed macaques inhabiting a deteriorating forest fragment included food items from a large variety of nonnative/pioneer plants in their diet. Tutin (1999) found that for four African primates (*Cercopithecus cephus*, *C. nictitans*, *Cercocebus albigena*, and *Colobus satanus*), the proportion of time spent feeding on fruit decreased while the proportion of time spent eating insects increased in forest fragments compared with continuous forest. Similarly, Lee (1997) found that groups of *Macaca nigra* that occupy more disturbed habitats consumed more insects than those in less disturbed areas.

Dietary diversity may also be affected by habitat quality because primates in forests with higher tree species richness are likely to have more foraging options and be less likely to experience periods of food scarcity than primates in more marginal forests (Poulsen et al., 2001). As a result, primates that occupy more marginal habitats may rely predominantly on a small number of critical food resources, or keystone species, such as figs, that play important roles in sustaining frugivores through periods of natural and "imposed" food scarcity (Leighton & Leighton, 1983; Terborgh, 1986; Kinnaird et al., 1999; Tweheyo & Lye, 2003).

Activity patterns should be assessed in relation to resource availability given that the partitioning of time involves tradeoffs between metabolic requirements and the acquisition of energy to fulfill those requirements (Oates, 1987). As the distribution and availability of food change (e.g., due to seasonal variations and/or habitat disturbance), time spent engaged in eating (an energy-accruing behavior) versus more costly behavior such as searching for or moving between food patches should also change (Kinnaird, 1990). In disturbed habitats, where there are typically fewer large trees (due to their removal), unevenness or high variability in fruit production is likely to be more pronounced than in undisturbed areas. This may result in foods being more patchy or clumped in their distribution, and primates may have to travel further and feed more to exploit such resources (Chapman, 1988; Overdorff, 1996). Fruit production may also be less in disturbed habitats due to fewer canopy and mid-canopy size trees (Lee, 1997). If habitat disturbance and its effects on resource availability are recent, population size may exceed the carrying capacity of the habitat, and therefore, one would expect foraging effort to increase among primates that utilize such disturbed habitats as they spend more time searching for the remaining food sources.

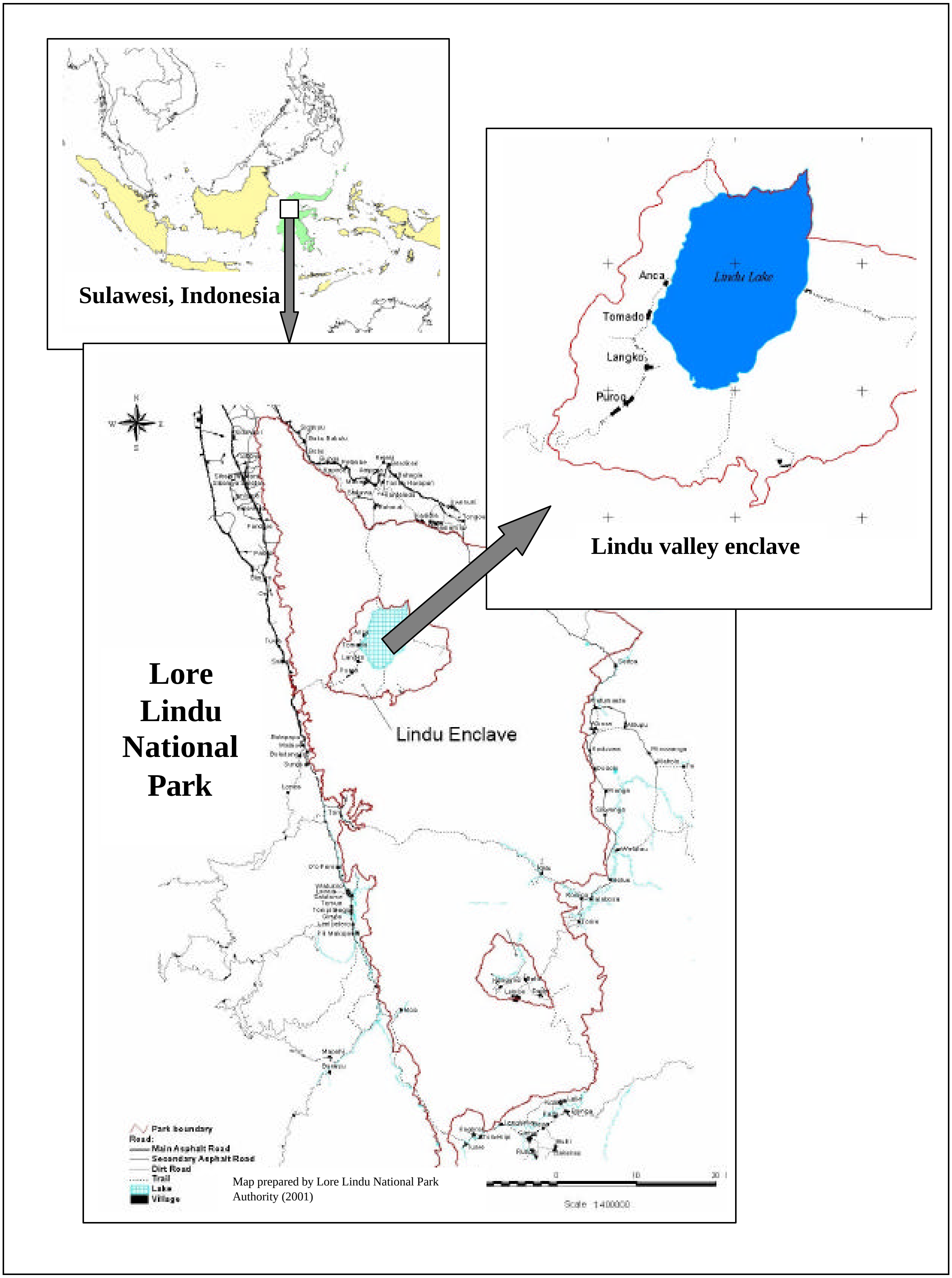
In this paper, I examine how Sulawesi Tonkean macaques (*Macaca tonkeana*) respond to anthropogenic habitat alteration in terms of their diet and activity patterns. The Tonkean macaque, which occurs only in Central Sulawesi, is one of the least-known species on the island with regard to socioecology and conservation status (Bynum et al., 1999). I studied two groups of *M. tonkeana* that occupied habitats with different levels of alteration to test predictions about diet and activity patterns. Anthropogenic habitat alteration was defined as the clearing of forest for agriculture and small-scale forest product collection, and is assumed to negatively impact habitat quality for nonhuman primates. Instead of relying on proxies of habitat quality, such as rainfall, I specifically quantified habitat quality by measuring the abundance, productivity, and distribution of food resources for Tonkean macaques. Due to expected differences in habitat quality for the two groups, the group living in heavily-altered habitat was expected to (1) consume less ripe fruit and more alternative type foods (e.g., insects, unripe fruit, leaves, flowers, and fungus), (2) show less dietary diversity, and (3) spend more time foraging, feeding, and moving, and less time resting and socializing, than the group in minimally-altered habitat.

METHODS

Study site

The research was conducted in the Lake Lindu valley enclave, which is situated at approximately 1,000 m.a.s.l., in Lore Lindu National Park (01°15' to 01°30' S; 119°50' to 120°20' E) in Central Sulawesi, Indonesia, from June 2002 to April 2004 (Fig. 2.1). Lore Lindu National Park, comprising a total area of 217,982 ha, was established in 1993 from two existing reserves and is designated as a UNESCO Man and the Biosphere Reserve. The park's flora is generally classified into two major vegetation types based on altitudinal distribution, with lowland forest (below 1000m) covering less than 10% of the park and montane forest (above 1000m) comprising the remaining 90% (Wirawan, 1981). Annual rainfall in the park averages between 2000-3000mm, which is evenly distributed over the year except for a slight maximum falling between November and April (Watling & Mulyana, 1981; Supriatna et al., 1992). In the

Figure 2.1. Map of Lore Lindu National Park, Sulawesi, Indonesia and outset of the Lindu valley enclave within the park



Map prepared by Lore Lindu National Park Authority (2001)

Lindu valley, average temperature was 21.9° C (range: 19.8 – 23.3° C), annual rainfall (Jan 2003 – Jan 2004) totaled 3113. 32 mm, and mean monthly rainfall was 212.4 mm (range: 85.5 – 773 mm).

Lore Lindu National Park has considerable conservation value in that it provides watershed protection for two major river catchment systems, the Lariang and the Gumbasa-Palu rivers (Wirawan, 1981). It also hosts a majority of Sulawesi's endemic mammals, including the mountain anoa (*Bubalus quarlesi*), the babirusa (*Babyrousa babyrussa*), two species of the marsupial cuscus (*Phalangar ursinus*, *P. celebensis*), three species of tarsier (*Tarsius spectrum*, *T. dianae*, *T. pumilus*), and one of the seven endemic macaques, *Macaca tonkeana*.

The park's status as a Biosphere Reserve means that some land use activities are allowed in buffer zone areas (i.e., a strip of forest that surrounds a core area of forest). The park is surrounded by 117 villages, 60 of which are located adjacent to these buffer zone areas (TNC, 2001). Approximately 70% of the population is indigenous to the area, while the remaining 30% are people who have moved into the area through both spontaneous immigration and the government transmigration programs (CSIADCP, 1997). As a result, a major pressure on the park is the increasing human settlement on adjacent lands and unauthorized harvesting of resources within the park.

Study animals

I studied two groups of Tonkean macaques whose habitats differed in levels of anthropogenic alteration (Table 2.1). The first group (hereafter, "Anca") occupied heavily-altered forest, characterized by frequent use by villagers (e.g., tree felling for livelihood needs) and conversion of forest to agricultural and agroforestry areas. The second group (hereafter, "CH") occupied minimally-altered forest (i.e., no agricultural areas, except one coffee agroforest garden on the southwestern edge of the group's range, yet frequent collection of rattan) inside the boundary of the National Park. Although levels of disturbance varied between the two study areas, both groups occupied lowland and hill forest (i.e., 0-1500m: Whitten et al., 2002). Because this research was the first to study the ecology and behavior of *M. tonkeana* at the chosen field site, a number of months (Anca: 7 months, CH: 5 months) were required prior to the start of systematic data collection to habituate the two groups to the point of tolerating human presence at a distance of less than 10 m.

Table 2.1. Group composition and habitat characteristics for the two study groups, Anca and CH

Feature	**Anca**	**CH**
Group Size (range)	6-9	26-28+
Group Composition[a]	3M, 2F, 1SJ, 2I Births: 2 Deaths: 3 (2 SJ, 1I) Emigrations: 1 (M)	9M, 9F, 5LJ, 3SJ, 1+U Births: 1 Deaths: 2 (1I, 1F)
Habitat alteration	Agroforestry (coffee, cacao) = 66% of group's range	One coffee agroforest garden at periphery of range = 2.1% of group's range
	Forest product collection (wood, rattan, wildlife)	Forest product collection (rattan, wildlife)

[a] At start of study, with information on births, deaths, and migrations during the course of the study. M = adult male, F = adult female, LJ = large juvenile, SJ = small juvenile, I = infant, U = unknown.

Forest composition and phenology

I collected data on forest structure and composition to assess differences in habitat quality between the ranges of the two groups. I defined habitat quality in terms of the abundance, diversity, productivity, and distribution of potential resources (i.e., for feeding, resting, and traveling). Several measures were used to determine habitat quality: species richness (i.e., number of tree species), tree diameter-at-breast height (DBH), tree basal area, the diversity and spatial distribution of potential food resources, and forest fruit abundance. A total of 40 vegetation plots, each 25m x 25m, were established per habitat. Twenty main plots were established at randomly selected points of intersecting trails within each group's range. The location of the main plots was structured such that the diversity of microhabitat types within the habitat was sampled. Replicate plots (also 25m x 25m) to each main plot were established 10 m from the edge of the main plot. In each plot, I identified and measured every tree = 10 cm DBH. In addition, because members of *Ficus* spp. have been identified as important food resources for other Sulawesi macaques (Kohlhaas, 1993; Lee, 1997; O'Brien & Kinnaird, 1997), I recorded the presence of all fig species in the vegetation plots. Each tree was assigned to a size class according to the following categories (Lee, 1997; Whitten et al., 2002): DBH ≤ 15cm = understorey (< 20m height); DBH 16-29 cm = mid-canopy (20-30m height); DBH ≥ 30cm = canopy (> 30m height). If tree samples could not be identified in the field, they were taken to the Herbarium Celebense at the University of Tadulako in Palu, Sulawesi, and the Bogor Herbarium in Bogor, Java.

I collected phenological data to determine whether forest fruit availability varies seasonally (i.e., across months of the year) and to assess whether there are differences in forest fruit availability between the two habitats. I tagged all trees = 20 cm DBH, all fig species, and any other tree species known to be a Sulawesi macaque food item (based on preliminary observations, and other studies of Sulawesi macaques) from 10 plots per habitat. These plots were chosen because they contained the greatest number of macaque food species. The phenological state of each tagged tree was estimated once a month on predetermined dates via visual examination with binoculars. Percentages of new leaves, flowering buds, flowers, unripe fruit, and ripe fruit were estimated (i.e., proportion of the total canopy covered by the item) and assigned an abundance score from 0-4, where 0 = 0% of the canopy, 1 = 1-25%, 2 = 26-50%, 3 = 51-75%, and 4 = 76-100%.

Feeding and behavioral observations

Following the initial period of habituation, each group was followed on three consecutive days each month for 15 months between January 2003 and April 2004. The only exceptions were April 2003, when no data were collected, and December 2003 – February 2004, when the groups were followed for 4, 5 and 4 days, respectively. Day follows began at 0600 and ended when the group settled in its sleeping tree, or when the group was lost and could not be relocated. Following Kinnaird (1990), every half hour, 10 minutes were spent taking a scan sample (Martin & Bateson, 1993) of the group, recording the following information for each individual located: (1) age/sex (5 classes: adult male, adult female, large juveniles, small juveniles, and infants), (2) food item if eating (and species if known): young leaves, mature leaves, fruit (ripe or unripe), stems, shoots and sprouts, seeds, flowers, insects, and crops (type & part), and (3) the first activity sustained for at least 5 seconds. Recorded activities included *moving, foraging, feeding, resting,* and *social/sexual* (Table 2.2). A total of 747 scans, over 373.5 hours across 45 days, were collected for the Anca group. For the CH group, 473 scans were collected during 236.5 hours across 36 days.

Table 2.2. Sampled behavioral repertoire of *Macaca tonkeana*

Behavior	**Definition**[a]
Moving	Locomotion, including walking, running, climbing, and jumping, excluding short movements during foraging and locomotion during activities such as playing.
Foraging	Moving slowly with attention directed toward a potential food source or manipulating substrates.

Feeding[b]	Ingesting and chewing food once it is located, or manipulating the contents of a cheek pouch.
Resting	Sitting, standing, or lying down while not involved in any other activity (including social activity), except autogrooming[c].
Social/Sexual	Composite category that includes *allogrooming*: an animal grooming or being groomed by another animal; *playing*: mock-chasing or mock-fighting; *sexual behavior*: mounting (non-copulatory and copulatory); and, *agonistic interactions*: the display of an aggressive behavior by an individual and an aggressive or non-aggressive response by the aggressee.

[a] Following Thierry (1985), O'Brien & Kinnaird (1997), and Thierry et al. (2000).

[b] If animals were observed feeding while simultaneously involved in another activity, the behavior was scored as feeding.

[c] If an individual was self-grooming, the behavior was recorded as resting-self-groom.

Data analysis

Forest structure and composition

A difference in tree abundance between the two habitats was tested with a two-tailed t-test. I calculated basal area (BA) for each tree from the DBH values using the following formula, and then dividing by 10,000 to convert to m^2 from cm^2: $BA = [0.5 X DBH]^2 x p$. These values were then divided by the number of hectares sampled to obtain basal area per hectare. Differences in total basal area and basal area of food trees between the two habitats were tested with two-tailed Mann-Whitney tests. I used a one-tailed t-test to test the prediction that mean DBH was greater in CH's habitat (minimally-altered) than in Anca's habitat (heavily-altered). To test the prediction that the CH habitat had a greater proportion of mid-canopy (16-29 cm DBH) and canopy (>30 cm DBH) trees, I used a one-tailed Fischer's Exact probability test. To test for significant differences in food species density and key food species density between the two habitats, I used Wilcoxon Signed Ranks tests.

I measured the diversity of tree species, and in particular potential macaque food resources, using the Shannon-Weaver index H' for each of the two habitats. The formula for the diversity index is:

$$H' = (N \log N - \sum n_i \log n_i) / N,$$

in which N is the total number of individuals, and n_i is the number of individuals of s_i (species i). The t-value ($t = H_1' - H_2' / v\ s_1^2 + s_2^2$) was then computed and compared to the critical value of Student's t to determine whether the diversity indices computed for each group were significantly different (Brower & Zar, 1984; Zar, 1996).

To measure the degree of dispersion (i.e., uniform, random, or clumped) of macaque food trees, I used Morisita's index of dispersion (I_d) (Morisita, 1962). Morisita's index provides a measure of the extent to which species are nonrandomly distributed among identically-sized plots. The index is calculated as: $I_d = n\ [?\ X^2 - N / N\ (N-1)]$, where n is the number of plots, N is the total number of individuals counted in all n plots, and $?\ X^2$ is the summation over all plots of the squares of the numbers of individuals per plot (Brower & Zar, 1984). The index ranges from $1/N$ to N, where values approaching 1.0 indicate a random distribution and those less than or greater than 1.0 represent uniform or patchy distributions, respectively. I then statistically assessed the departure of the observed dispersion pattern from randomness by computing, $?^2 = n?\ X^2 / N - N$, and comparing this chi-square value to the appropriate critical value.

Forest fruit availability

To determine whether fruit production differs between the two habitats, I computed an index of fruit availability from the phenological data. The index involved the calculation of a mean species abundance score for each tree species within the phenology plots known to be a macaque food species. Because species density can influence habitat-wide fruit availability

(Chapman et al., 1994), I multiplied the mean species abundance scores by species density to derive a composite score. An index of total fruit availability was then derived by taking the sum of the composite species scores and dividing by the number of species in the sample (Wieczkowksi, 2003). This index was calculated using ripe fruit abundance scores and using lumped scores for ripe and unripe fruit.

I used Kolmogorov-Smirnov tests to determine whether rainfall and forest fruit production exhibited uniform distributions across the study period. To determine whether rainfall was correlated with forest fruit availability I calculated Spearman rank-order coefficients (r_s). I tested for differences in fruit availability between the two habitats using one-tailed Mann-Whitney tests.

Diet and activity patterns

I measured annual dietary diversity using the Shannon-Weaver index, *H'* (Brower & Zar, 1984) for all food tree species, as described above. I calculated the mean percent contribution of each diet item weighted by the number of feeding records obtained for each group over the study period. To estimate the amount of time spent in five activities (forage, rest, move, social, feed), I divided the number of records of each behavior by the total number of records (observations) per day and multiplied by 100. Days in which there were fewer than 15 behavioral observations for the group were excluded from the analysis. I used two-way ANOVA techniques to test for the predicted differences in diet composition and activity patterns between the two groups, with group (i.e., habitat) as the main effect. Season, which represented diet and behavioral data divided into four periods (Jan – Mar 2003, May – Aug 03, Sept – Dec 03, Jan – Apr 04), was only added as a blocking factor because the main interest was the habitat effect. Arcsine transformations were performed on the proportional diet and activity data to meet assumptions of normality and equal variances required by ANOVA techniques (Sokal & Rohlf, 1981). Because there were within-group and between-group differences in the total number of feeding records and total number of behavioral observations collected per day throughout the data collection period, I used the Weighted Least Squares (WLS) function in the ANOVA models, where the weighted variables were total number of feeding records for the monthly sample (3-day scans), for the diet data, and total number of observations for the particular sample day, for the activity data. For all statistical tests, results were considered significant at $P = 0.05$.

RESULTS

Forest composition

A total of 2.5 ha were sampled in each group's habitat (Table 2.3). Tree abundance was significantly greater in the CH habitat than in the Anca habitat (t-test, df = 78, $P < .001$). Total basal area was not significantly different between the two habitats (Mann-Whitney, Z = -1.78, $P = .075$).

Table 2.3. Sampling effort and forest composition attributes in the two habitats

Feature	**Anca**	**CH**
Area sampled (ha)	2.5	2.5
No. of families	54	53
No. of species (no. of food species)	156 (44)	175 (39)
Total no. of trees enumerated	813	1301
Total tree density (trees/ha)	325.2	520.4
Basal area (m^2/ha)	33.54	39.33

The distribution of trees across different size classes for the two habitats was not uniform ($?^2 = 35.89$, df = 2, $P < .001$; Fig. 2.2). In contrast to what was predicted, the CH habitat did not have a significantly greater proportion of mid-canopy sized (1-tailed, $?^2 = 0.19$, df =1, $P = .348$) or canopy-sized (1-tailed, $?^2 = 28.17$, df = 1, $P = .999$) trees than the Anca habitat. There was a significant difference in mean DBH between the two habitats, but in the opposite direction than predicted; mean DBH was statistically greater in Anca (27.64 cm, *n* =723) than in CH (23.92 cm, *n* =1168) (t-test, df =1889, *P* <.001).

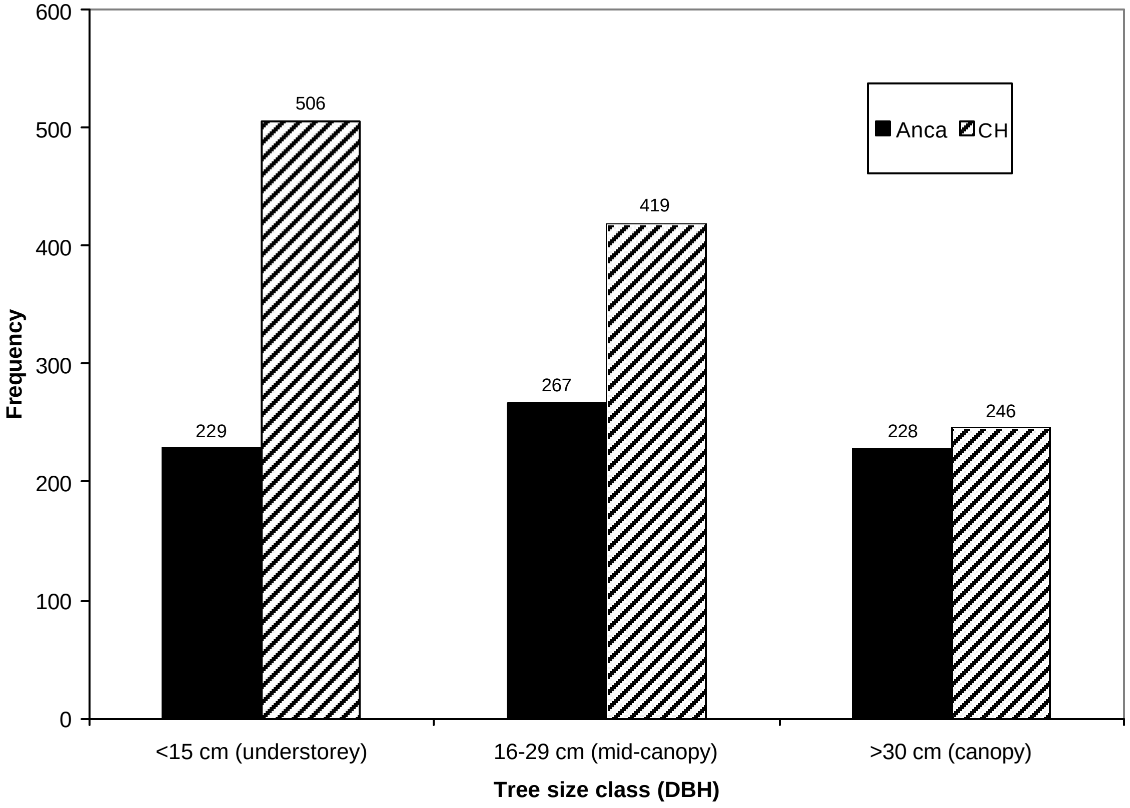


Figure 2.2. Distribution of trees across three DBH size classes in the two habitats

Mean DBH of food species was also significantly greater in Anca habitat (29.57 cm) than in CH habitat (20.55 cm) (1-tailed t-test, df = 605, *P* <.001; Table 2.4). Basal area of food species was not significantly different in the two habitats (Mann-Whitney, Z = -0.414, *P* = .679). Food species density was not significantly different in the two habitats (Wilcoxon Signed Ranks test, Z = -1.259, *P* = .208). Key food species density, however, was significantly greater in the

CH habitat than the Anca habitat (Wilcoxon Signed Ranks test, Z = -2.562, *P* = .01) (Tables 2.4 & 2.5).

Table 2.4. Summary of macaque food species data per habitat

Feature	**Anca**	**CH**
Mean DBH of all food species (cm)	29.56	20.55
Basal area of all food trees (m^2/ha)	10.06	11.85
All food species density	120	212
Key food species[a] density	34.8	112.8

[a] Key food species: *Elmerillia tsiampacca*, *Ficus* spp., *Pandanus* spp., *Ficus benjamina*, *F. virgata*, *Pinanga* spp., and *Arenga pinnata*

Species diversity was significantly greater in Anca's habitat (*H'* = 1.96) than in CH's (*H'* = 1.81) for all tree species (t = 5.79, df = 1831, *P* <.001) and for food species (Anca = 1.42, CH = 1.19; t = 6.53, df = 780, *P* <.001).

The majority of food species in both habitats were patchily or randomly distributed in space (Table 2.5); 50% and 43% were randomly distributed, and 33% and 35% were patchily distributed, in the Anca and CH habitats, respectively. Only one species (*Pinanga sp.*) showed a uniform spatial pattern in the CH habitat. Three species, *Garcinia parviflora*, *Ficus sagittata*, and *Streblus elongatus*, showed a more patchy distribution in the Anca habitat than the CH habitat, despite similar or higher tree densities in the CH habitat. Of the seven species that were more patchily distributed in the CH habitat than the Anca habitat, four of these species (*Ficus benjamina*, *Antidesma bunius*, *Ficus obscura*, *Musa celebica*) were either extremely rare (0.4 trees/ha) or not present in the Anca habitat. Seventeen percent and 20% of food species in the Anca and CH habitats, respectively, were rare, occurring at densities of less than one individual per sampled area (2.5 ha).

Table 2.5. Density and degree of clumping (Morisita's index of dispersion, I_d)[a] of all food trees in Anca and CH habitats (2.5 ha per habitat). If the I_d is significantly greater or less than unity using the ?^{2} test, the species is considered clumped or evenly distributed in space, respectively. If I_d is not significantly different from unity the species is considered randomly distributed.

	Anca			**CH**		
Taxon	**Density**	**I_d**	**P**	**Density**	**I_d**	**P**
ANARCARDIACEAE						
Mangifera foetida	2.4	0	ns	0	-	-
BURSERACEAE						
Canarium commune	1.6	2	ns	0.4	*	*
CLUSIACEAE						
Cratoxylon celebicum	0.4	*	*	0	-	-
Garcinia parviflora	3.2	7.86	<.001	3.2	1.43	ns
ELEAOCARPACEAE						
Eleaocarpus musseri	0	-	-	1.2	0	ns
EUPHORBIACEAE						
Antidesma bunius	0.4	*	*	5.6	2.64	<.005
Bridelia glauca	0.8	0	ns	1.2	0	ns
FAGACEAE						
Lithocarpus sp.	2	0	ns	6.4	1.5	ns
LAURACEAE						
Cinnamomum sp. 1	0	-	-	0.4	*	*
Cinnamomum sp. 2	0	-	-	0.4	*	*
Cryptocarya crassinerviopsis	2.4	13.33	<.001	2.8	2.86	<.05
Litsea mappcea	1.2	0	ns	0	-	-
MAGNOLIACEAE						
Elmerillia ovalis	2.4	1.33	ns	3.6	0	ns
Elmerillia tsiampacca	2	2	ns	2.4	0	ns
MELIACEAE						
Dysoxylum sp.	0.4	*	*	3.2	1.43	ns
Lansium sp.	0.4	*	*	0	-	-
MORACEAE						
Artocarpus teysmanii	2.4	1.33	ns	0	-	-
Artocarpus vriescana	3.2	0.95	ns	0.4	*	*
Ficus annulata	0	3.81	<.025	0	-	
Ficus benjamina	0.4	*	*	4.8	2.12	<.05
Ficus chrypcopsis	1.2	6.67	<.05	0.8	20	<.01
Ficus drupacea	0	*	*	0.4	*	*
Ficus glubosa	0.8	20	ns	0.4	*	*
Ficus heteropleura	0.8	0	ns	0	-	-
Ficus obscura	0	-	-	1.2	6.67	<.05
Ficus obscura var. angustata	0	-	-	2.4	0	ns
Ficus sagittata	2.8	3.81	<.025	4	2.22	ns
Ficus spp.	6.8	0.88	ns	10.4	0.8	ns

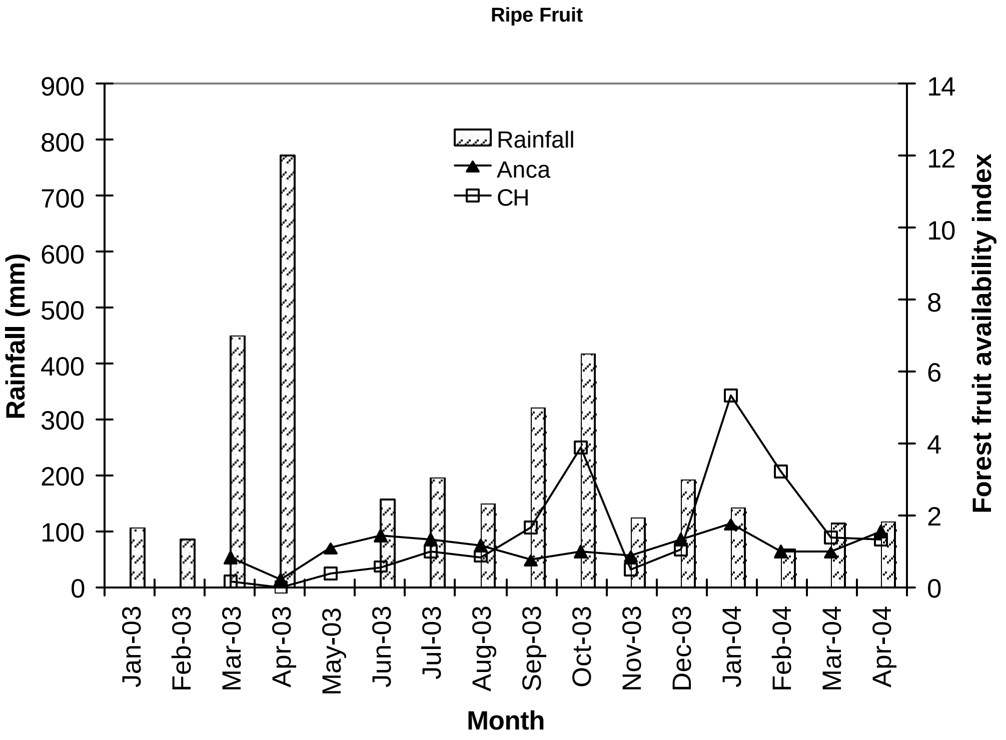
Ficus subulata	1.6	0	ns	5.6	1.98	<.05
Ficus tinctoria	0.8	0	ns	0	-	-
Ficus var. arsustata	0	4	ns	1.6	3.33	ns
Ficus variegata	2.8	0.95	ns	0	-	-
Ficus virens	1.6	0	ns	2	2	ns
Ficus virgata	0.8	0	ns	1.2	6.67	<.05
Streblus elongatus	2	4	<.05	0.8	0	ns
MUSACEAE						
Musa celebica	0	-	-	2.8	8.57	<.001
MYRISTICACEAE						
Horsfieldia pachythyrsa	2	0	ns	5.6	1.76	ns
Knema cf. *cinerea*	0.4	*	*	0	-	-
MYRSINACEAE						
Ardisia forstenii	1.2	20	<.001	0	-	-
PALMAE						
Areca vestiaria	10	3.93	<.001	11.2	2.43	<.001
Arenga pinnata	8.8	1.99	<.005	0.4	*	*
Caryota mitis	1.2	0	ns	0.8	20	<.01
Caryota sp.	4	0.44	ns	1.6	0	ns
Pinanga casea	8.8	2.69	<.001	0	-	-
Pinanga sp.	6	2.29	<.01	37.2	0.86	<.005
PANDANACEAE						
Pandanus sp.	1.2	20	<.001	56.4	3.5	<.001
RUBIACEAE						
Timonius teysmannii	0.4	*	*	3.6	1.11	ns
SABIACEAE						
Melisoma sumatrana	2	4	<.05	10.4	2.83	<.001
SAPINDACEAE						
Harpulia cupanioides	1.2	0	ns	0.4	*	*
STYRACACEAE						
Bruinsmia styracea	3.6	2.22	ns	2	2	ns
URTICACEAE						
Dendrocnide stimulans	4	2.67	<.025	13.2	1.82	<.001
Villebrunea rubescens	17.2	1.95	<.001	2	6	<.005

[a] Values approaching 1.0 indicate a random distribution, and those less than or greater than 1.0 represent uniform or patchy distributions, respectively. * Denotes the sample size for the species was 1, and thus the Morisita's index was not calculated for these species.

Climate and forest phenology

There were no distinct wet or dry seasons in the Lindu valley, as rain fell throughout the year. Rainfall did, however, vary significantly from a uniform distribution, with peaks in March-

April 2003 and Sept-Oct 2003 (Kolmogorov-Smirnov test, Z = 1.845, *P* = .002; Fig. 2.3). Forest fruit availability in the two habitats was not correlated with rainfall (All Fruit, Anca: *P* = .128, CH: *P* = .209; Ripe Fruit, Anca: *P* = .184, CH: *P* = .194). In both habitats, total fruit availability (ripe and unripe fruit) did not differ significantly from a uniform distribution (Kolmogorov-Smirnov test, Anca: Z = 1.043, *P* = .227; CH : Z = 1.010, *P* = .260; Fig. 2.3), nor did ripe fruit availability vary seasonally in the Anca habitat (Kolmogorov-Smirnov test, Z = 1.103, *P* = .257). Ripe fruit availability in the CH habitat did differ from a uniform distribution (Kolmogorov-Smirnov test, Z = 1.791, *P* = .003; Fig 2.3). Total fruit availability (lumped ripe and unripe fruit) across months was significantly greater in CH than in Anca (Mann-Whitney, Z = 1.976, *P* = .025; Fig. 2.3).



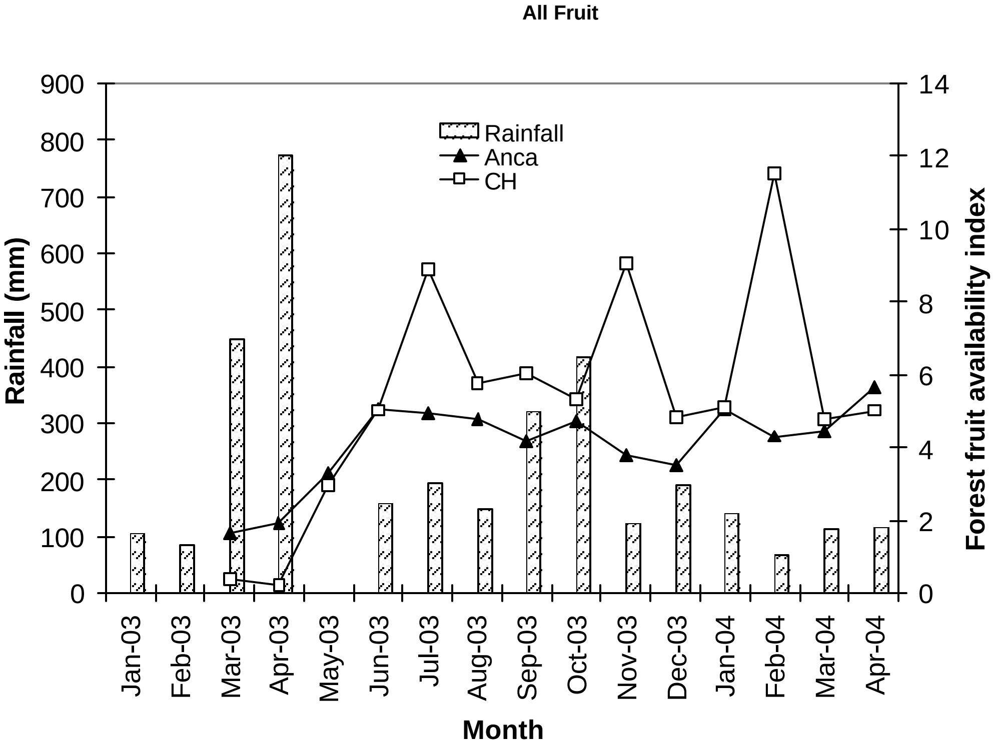


Figure 2.3. Temporal distribution of rainfall and forest fruit availability (ripe fruit and all fruit) in the two groups' habitats

Diet

For both groups, ripe fruit made up the largest proportion of the diet (Table 2.6). For the CH group, ripe fruit accounted for a significantly greater proportion of the diet than for the Anca group (*F* = 5.48, df = 1, *P* = .014; Table 2.6, Fig. 2.4). For the Anca group, insects and alternative food items, as a whole, accounted for a significantly greater proportion of the diet than for the CH group (insects: *F* = 7.35, df = 1, *P* =.002; alternative foods: *F* = 5.51, df = 1, *P* = .014; Table 2.6, Fig. 2.4).

Table 2.6. Mean percent contribution[a] of each food item to total diet by group

Food Item	**Anca**		**CH**	
	%	**SE**	**%**	**SE**
Ripe fruit	66.8	4.4	79.8**	4.9
Insects	14.6*	2.4	5.6	2.7
Unripe fruit	9.9	3.2	4.6	3.6
Young leaves	1.6	1.0	4.2	1.2
Shoots & sprouts	1.8	1.0	3.1	1.1
Fruit (unknown stage)	1.4	0.5	1.4	0.6
Mature leaves	1.3	0.4	0	0
Fungus	1.0	0.3	0.3	0.4
Flowers	0.8	0.5	0.8	0.5
Stems	0.3	0.2	0	0
Other[b]	0.4	0.4	0.4	0.4

[a] Weighted by number of feeding records per sample day. Total number of feeding records: Anca = 479, CH = 359. [b]Other: exudates, crustaceans. * $P < .05$ ** $P < .005$

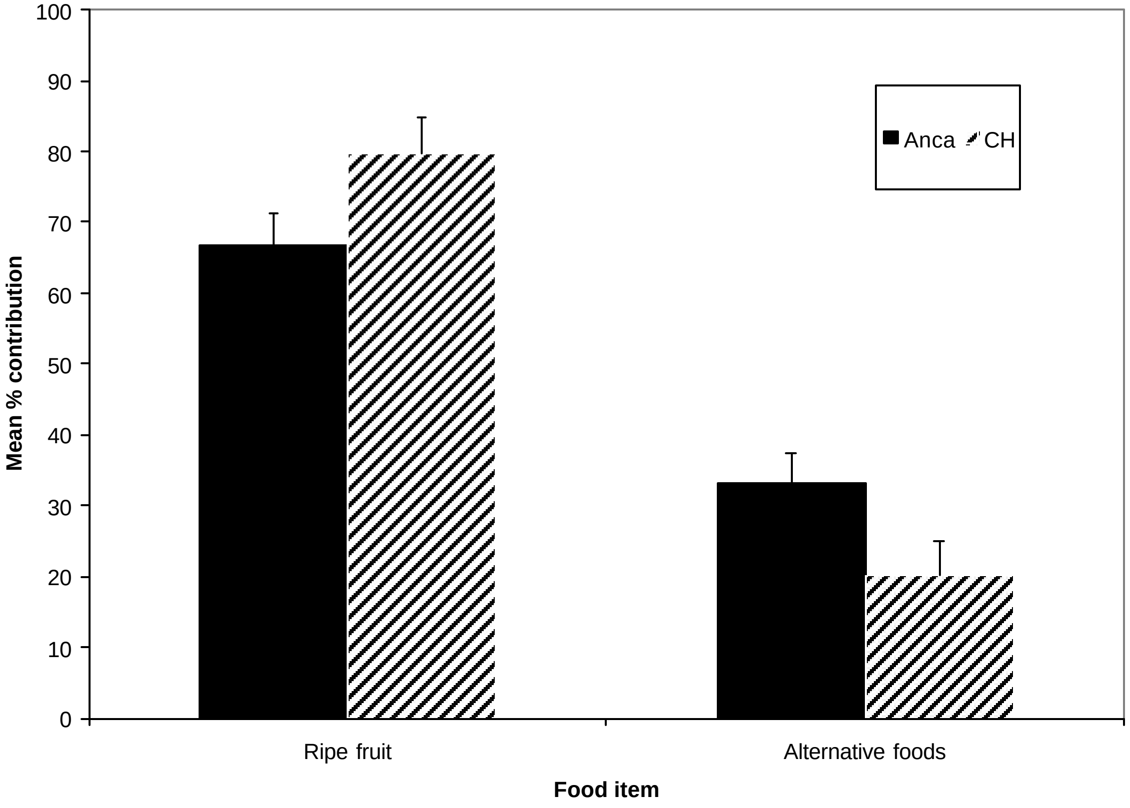


Figure 2.4. Mean percent contribution of ripe fruit and alternative foods to total diet per group. Error bars represent plus one standard error from the mean.

At least 54 and 56 species of plant foods were consumed by the CH and Anca groups, respectively (Table 2.7).

Table 2.7. Plant food species included in the diet of *Macaca tonkeana* (with local name of the species, specific group observed consuming the species, and plant part consumed).

Family **Genus & Species**	**Local Name**	**Plant Part**[a]	**Group**[b]
Anacardiaceae			
Buchanania arborescens		FR	CH
Mangifera foetida	Mangga	FR	A
Apocynaceae			
Willughbeia flavescens		FR	CH
Araceae			
Photos rumphii	Tali vanilla hutan	FR	A, CH
Arecaceae			
Calamus sp.	Atabose	SS	A
Calamus zollingeri	Rotan batang	SS	CH
Daemonorops robusta		FR	CH
Asteraceae			
Blumea lacera	Rumput	ML	A
Crassocephalum crepidioides	Rumput	ML	A
Balsaminaceae			
Impatiens sp.		FL	A
Burseraceae			
Canarium commune	Pakanangi	FR	A
Clusiaceae			
Cratoxylon celebicum	Tomondu	FR	A
Garcinia parvifolia	Maro	FR	A, CH
Elaeocarpaceae			
Eleaocarpus musseri	Pakela	FR	CH, K
Euphorbiaceae			
Antidesma bunius	Tamba	FR	CH, K
Bridelia glauca	Koulao	YL	A
Fagaceae			
Lithocarpus sp.	Palili	FR	A
Icacinaceae			
Iodes cirrhosa	Tali hutan	FR	A
Lauraceae			
Cinnamomum sp.		FR	A, CH
Cryptocarya crassinerviopsis	Bakankara	FR	CH
Litsea mappacea		FR	A
Liliaceae			
Ploemele angustifolia	Topeliu	FR	K
Magnoliaceae			

Elmerillia ovalis	Uru (Cempaka)	FR	A, CH
Elmerillia tsiampacca	Takasa (Cempaka)	FR	A, CH, K
Meliaceae			
Dysoxylum nutans	Langsat, lonca ibo	FR	A
Dysoxylum sp.	Lasa	FR	CH
Moraceae			
Artocarpus teysmannii	Tea	FR	A, K
Artocarpus vriescana	Baloli	FR	A
Ficus benjamina	Beringin	FR	A, CH
Ficus chrycopsis		FR	CH
Ficus chrysolepis		FR	CH
Ficus drupacea		FR	A, CH
Ficus elmeri		FR	A, CH
Ficus glubosa		FR	CH
Ficus heteropleura		YL	A
Ficus obscura		FR	A, CH
Ficus obscura var. *angustata*		FR	CH
Ficus pilosa		FR	A
Ficus pubinervis		FR	A
Ficus sagittata		FR	A, CH
Ficus spp.		FR, SS, YL	A, CH
Ficus subulata		FR	A
Ficus tinctoria		FR	A, CH
Ficus variegata		FR	A
Ficus virens		FR	CH
Ficus cf. *virens*		FR	CH
Ficus virgata		FR, YL	A, CH, K
Streblus elongates		FR	A, CH
Myristicaceae			
Horsfieldia pachythyrsa		FR, YL	A, CH
Knema cf. *cinerea*	Koura	FR	A
Myrsinaceae			
Embelia sp.		FR	CH
Ardisia forstenii		FR	CH
Nephrolepidaceae			
Nephrolepsis biserrata		ML (fern)	A
Palmae			
Areca vestiaria	Pinang merah	FR, SS	A
Arenga pinnata	Enau	FR	A, CH, K
Caryota mitis	Mpire	FR	CH
Caryota sp.	Mpora	FR, SS	A, CH
Pinanga caesea	Pinang hitam	FR, SS	A, K
Pinanga sp.	Pinang hitam	FR, SS	A, CH
Pandanaceae			
Pandanus spp.	Pandan	FR, SS	A, CH, K
Piperaceae			

Piper aduncum		FR	#
Rubiaceae			
Anthocephalus indicus		FR	A, CH
Timonius teysmanii	Kalambio	FR	A, CH
Rutaceae			
Harpulia cupanioides	Sipu	FR	K
Sabiaceae			
Melisoma sumatrana		YL	A
Styracaceae			
Bruinsmia styracea	Kalia	FR	A, CH
Symplocaceae			
Symplocos sp.		FR	A
Urticaceae			
Dendrocnide stimulans	Delata	YL	CH
Leucosyke capitellata		FL	A
Poikilospermum suaveolens		FR	CH
Villebrunea rubescens	Marangkapi	FL, YL	A
Zingiberaceae			
Eltingera sp.	Bunga	FL	A

[a] FR = Fruit, FL = Flower, YL = Young leaves, ML = Mature leaves, SS = Shoots & Sprouts.
[b] A = Anca, CH = Camp Hutan, K = Kalora (The Kalora group was followed for 10 months in attempt to habituate for systematic behavioral observations. I conducted scan samples on this group in Mar 2003, then again May –Nov 2003, but the data obtained were not sufficient to include in any analyses.).
*Ad libitum observations.
Macaque group observed feeding on the side of a road outside of the National Park.

The top food species differed between the two groups (Tables 2.8). For the CH group, species from three genera (*Elmerillia tsimapacca*, *Ficus* spp., and *Pandanus* spp.) accounted for more than 50% of the diet. For the Anca group, only one species, *Arenga pinnata*, accounted for 52% of the diet on plant species.

Table 2.8. Top 15 food tree species and percent contribution to plant species diet for the two groups

ANCA		**CH**	
Species	**%**	**Species**	**%**
Arenga pinnata	52	*Elmerillia tsiampacca*	20.7
Ficus spp.	10.9	*Ficus* spp.	19.7
Artocarpus teysmannii	4.5	*Pandanus* spp.	12.5

Artocarpus vriescana	3.1	*Ficus* cf. *virens*	9.4
Elmerillia tsiampacca	2.8	*Ficus benjamina*	7.2
Ficus pubinervis	2.5	*Ficus virgata*	6.3
Cinnamomum sp.	2.0	*Pinanga* spp.	4.1
Bruinsmia styracea	2.0	*Eleaocarpus musseri*	3.1
Pinanga spp.	1.9	*Ficus elmeri*	1.6
Ficus heteropleura	1.7	*Ficus tinctoria*	1.6
Caryota sp.	1.7	*Ficus chrycopsis*	1.6
Ficus pilosa	1.4	*Arenga pinnata*	1.3
Ficus sagittata	1.1	*Ficus sagittata*	1.3
Ficus subulata	1.1	*Ficus drupacea*	.9
Streblus elongatus	1.1	*Ficus virens*	.6

Annual dietary diversity of plant food items was significantly greater for the CH group ($H' = 1.19$) than for the Anca group ($H' = 1.08$) (t = -2.18, df = 731, $P < .01$). Dietary diversity of all food items was also significantly greater for the CH group ($H' = 1.22$) than for the Anca group ($H' = 1.14$) (t =-1.85, df = 838, $P < .05$).

Activity patterns

There were significant between-group differences in mean percent time spent in the different activities (Fig. 2.5). As predicted, time spent foraging was significantly greater in the Anca group than in the CH group (ANOVA, F = 6.02, $P = .008$). In contrast to what was predicted, the Anca group did not spend a significantly greater proportion of time moving (F = 19.85, $P = .999$) or resting (F = 3.56, $P = .969$). Instead, the results are significant in the opposite direction: percent time moving was significantly greater for the CH group, and percent time resting was significantly greater for the Anca group. There were no significant differences in time spent feeding (F = 1.07, $P = .152$) and socializing (F = 0.5, $P = .242$) between the two groups.

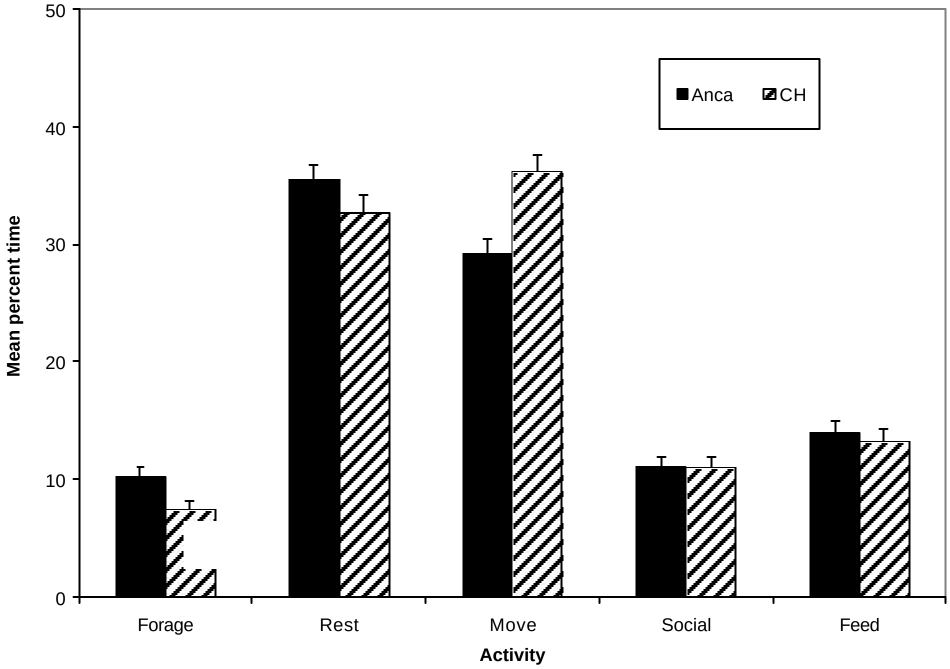


Figure 2.5. Mean percent time spent by each group in the five activities. Error bars represent plus one standard error of the mean.

DISCUSSION

In this study, anthropogenic habitat alteration was expected to result in lower quality habitat for Tonkean macaques. In contrast to what was predicted, two key features often used to measure habitat quality, mean DBH and tree species diversity, were significantly greater in the heavily-altered habitat (Anca) than the minimally-altered habitat (CH). The observed difference in mean DBH may be due to the greater number of new growth trees (<10 cm DBH) found in the CH habitat than the Anca habitat; for in the Anca habitat, these are primarily the trees felled when villagers convert forest areas to agricultural gardens. Higher species diversity in the Anca habitat may reflect the fact that secondary growth areas are often characterized by higher levels of plant diversity due to the presence of pioneer species (Chapman, 1987; Johns, 1988; Corlett, 1995). What these results suggest is that other key features that relate specifically to the abundance and productivity of important food resources may be better indicators of habitat quality; a more food species rich and dense habitat may ultimately provide more foraging options than a habitat where only species diversity is high (Poulsen et al., 2001). In this study, key food species density was significantly greater in the minimally-altered CH habitat than in the heavily-altered Anca habitat. Spatial distribution of food resources was similar in the two habitats, but there were a number of important food species that were rare or non-existent, and exhibited a more patchy distribution in the Anca habitat than in the CH habitat. Fruit production was fairly uniform across the research period in both habitats, indicating that there are no "natural" periods of resource scarcity for the macaques. Total fruit production was, however, significantly less in the Anca habitat than in the CH habitat, indicating that the Anca habitat may be subject to "imposed" food scarcity from overall lower resource availability. In sum, the results suggest that the habitat within the Anca group's range should be characterized as lower in quality than CH's habitat.

Diet composition and activity patterns in relation to habitat quality

Diet composition, when viewed in relation to the differences between the two habitats, is primarily linked to habitat quality for Tonkean macaques. The Anca group, which occupies heavily-altered habitat, consumed less ripe fruit and more alternative food items than the CH group. These results may reflect the lower densities of key food species in their habitat. Although ripe fruit constituted the largest proportion of the Anca group's diet, they did consume a significantly greater proportion of insects than did the CH group, suggesting that they may be supplementing their diet with a higher intake of insects. Lee (1997), in his research on *Macaca nigra*, observed a similar pattern with groups occupying habitats with different levels of disturbance. Insect availability has been shown to be greater in more disturbed habitats (Brown & Hutchings, 1997; Spitzer et al., 1997; Fiedler & Schulze, 2004, but see Hames & Hill, 2000), and although not measured in this study, such differences in insect availability may have contributed to the observed differences in diet composition between the two groups. Lower dietary diversity observed in the Anca group may also reflect lower densities of key macaque food species in their habitat. In contrast, the CH group, whose habitat provides greater foraging options and who may be depleting food patches more quickly due to their larger group size (Waser, 1977; van Schaik et al. 1983), may be visiting more trees, resulting in a greater dietary diversity.

The extent of the Anca group's reduced dietary diversity in response to changes in habitat quality is evident by the finding that it relies disproportionately on one species for its diet; more than 50% of the plant species diet was comprised of the fruits of a single palm, *Arenga pinnata.* Lee (1997) observed that groups of *M. nigra* occupying severely disturbed habitats also heavily exploited this species. Lee (1997) suggests, however, that this palm may have several drawbacks for macaques, in that only a few individuals are able to exploit the resource because the trees fruit asynchronously and produce a small number of fruit at a given time. In this study, at any given time during the research period there were one or more *Arenga* trees fruiting, and because of the small size of the Anca group, the entire group could feed on the fruits of the tree in one feeding bout, and would often even return to the same tree within the same day. The high density of *Arenga pinnata* in the Anca habitat (8.8 palms/ha) and the fact that the fruits are available year round and thus offer a stable source of calories, suggests that this palm may act as a keystone resource (Terborgh, 1986) for Tonkean macaques that occupy human-modified habitats. These results therefore suggest that the potential value of a resource may depend on the particular ecological characteristics of the resource *in relation to* other factors such as group size. The Anca group may be disproportionately using this resource because of its high density, because other food trees have lower densities, but also because they *can*; their small group size permits the utilization of this resource by all members and thus diminishes the need to travel and forage elsewhere.

Figs (*Ficus* spp.), which are very high in abundance in Lore Lindu National Park (33.2 figs/ha) compared with other Indonesian forests (6.6 figs/ha, East Kalimantan: Leighton & Leighton, 1983; 7-10 figs/ha, North Sulawesi: Kinnaird et al., 1999), were also important foods for both groups. Figs therefore may also serve as keystone food sources for Tonkean macaques, particularly for groups living in disturbed habitats where fig species often thrive (Plumptre & Reynolds, 1994; Estrada et al., 1999; Fashing, 2001).

Measures of habitat quality, such as diet quality, food abundance, and the temporal and spatial distribution of food, have been shown to strongly influence the amount of time nonhuman primates spend in different activities (Kinnaird, 1990; Overdorff, 1996; O'Brien & Kinnaird, 1997; Poulsen et al., 2001). Group size is also one of the most important influences on primate activity budgets; primates living in larger groups are expected to feed more, scan less for predators, spend more time foraging, and travel more and further than smaller groups (van Schaik et al., 1983; Chapman, 1988; Isbell & Young, 1993; Menon & Poirier, 1996). In this study, it is possible that the small group size of the Anca group is the direct result of diminishing habitat quality impacting mortality or producing fission of a once larger group. The benefits accrued from group living will no longer outweigh the costs (e.g., competition, increased energy expenditure, increased social tension), if foraging efficiency decreases and within-group competition increases as a result of lower resource availability (Terborgh, 1983; van Schaik et al., 1983; Chapman, 1990). Large groups can respond to habitat alteration and diminishing habitat quality by employing a number of non-mutually exclusive strategies: increasing their home range size (Lee, 1997; Wieczkowski, in press), fissioning—where larger groups split and form new smaller groups that can forage in smaller food patches without depleting the patches (van Schaik et al., 1983; Johns, 1986; Rodman, 1988), and by exploiting new foods or foods of lower quality (Singh et al., 2001).

When situated in this context, the observed pattern of how the Anca group partitions its time is more readily interpreted. The greater proportion of time spent foraging by the Anca group most likely reflects the necessary adjustment in the search for food in a habitat where resource availability is lower. In such disturbed habitats, with fewer, and more patchily distributed, resources available (Johns, 1988), it is also expected that groups will spend more time traveling because they need to travel further and longer to find food sources (Chapman, 1988; Isbell & Young, 1993; Overdorff, 1996). In this study, the results were opposite to what was predicted: the CH group spent significantly more time traveling than the Anca group. That the Anca group traveled less and rested more in a habitat of poorer quality may reflect an interaction between group size and habitat quality; the Anca group can only utilize resources that remain in its habitat, which may be clustered, and because of their small group size, they do not exhaust these remaining resources as quickly as a larger group might, thus reducing the need to extend travel. Concomitantly, that the Anca group spent less time moving in their habitat explains why more time was available for resting and socializing. In contrast, the CH group may spend more time moving because in their habitat there are more resources available to exploit, and because their larger group size means that they will need more resources and will more quickly deplete these resources (Waser, 1977; Chapman & Chapman, 2000).

The finding that the Anca group spent a similar amount of time feeding as the CH group, despite its smaller group size, may be linked to its diet in a habitat of lower quality; one which included significantly more alternative food items, and more than 50% of which was comprised of the fruits of one palm species. The Anca group may need to eat more of these items to obtain sufficient nutrients, and it is also possible that the processing times of these items are longer, thus resulting in more time spent feeding than would be expected given its small group size.

Although long-term studies of multiple groups within a species are necessary to fully document what is characteristic and what is possible of a species, the results from this study suggest that Tonkean macaques may be responding to anthropogenic habitat alteration by exploiting keystone resources that dominate human-altered areas (e.g., *Arenga pinnata*), by being flexible in their diet by incorporating more alternative food items, such as insects, fungus, crustaceans, leaves and shoots of colonizing weeds (e.g., *Blumea lacera*), and by adjusting their activity budgets. Furthermore, the small group size observed for the group living in heavily-altered habitat (Anca group) may be the optimal size in which foraging efficiency is maximized for that habitat (Stacey, 1986), and thus may be the response, in conjunction with dietary and behavioral flexibility, to disturbance of their habitat. Such ecological and behavioral flexibility may allow Tonkean macaques to persist in heavily-altered environments.

These results should not be interpreted, however, as an indication that nonhuman primates endure human-induced habitat alteration without negative effects. A reliance on a small number of species for a majority of the diet may be a limited strategy for Tonkean macaque groups living in areas where disturbance is regular and increasing, particularly if those key food species represent tree species highly valued and utilized by villagers for their livelihood needs. The *Arenga pinnata* palm is highly valued by villagers, but in its *living* form (Riley, in prep. c);

it is not only protected for its resources but also in some areas of Sulawesi planted by local farmers (Mogea et al., 1991). cultivated This palm may therefore become an even more important resource for macaques in human-altered areas as other important food species, such as *Elmerilla tsiampacca* and *Artocarpus teysmannii,* are felled for lumber and/or dug-out canoe construction by villagers (Riley, in prep. c).

It is also possible that heavily-altered areas like the Anca habitat are sink habitats (i.e., where local mortality exceeds local reproductive success (Meffe & Carroll, 1997)), and therefore do not ultimately contribute to the viability of Tonkean macaque populations. Although both of the adult females in the Anca group exhibited one-year interbirth intervals during the study period (see Table 2.1), the fact that one infant and two juveniles from the Anca group died during this period is at least suggestive that survivorship may be negatively affected by the demonstrated reduced habitat quality from disturbance in their range. Efforts to conserve intact, minimally-altered habitat for nonhuman populations must therefore remain a top priority.
The results from this study do, however, point to the potential conservation value of human-modified landscapes as vital refuges for nonhuman primates (Chapman & Lambert, 2000; McCann et al., 2003). In the contemporary world, where human and nonhuman primate habitats and needs are increasingly interwoven, such environments may be necessary for effective conservation.

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CHAPTER 3

RESPONDING TO ANTHROPOGENIC HABITAT ALTERATION: FLEXIBILITY IN RANGING PATTERNS AND HABITAT USE OF *Macaca tonkeana* IN LORE LINDU NATIONAL PARK, SULAWESI, INDONESIA[1]

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[1] Riley, E.P. To be submitted to *American Journal of Physical Anthropology*.

ABSTRACT

The purpose of this study was to examine how the Sulawesi Tonkean macaque (*Macaca tonkeana*) responds in terms of its ranging patterns and habitat use to anthropogenic habitat alteration in Lore Lindu National Park, Sulawesi, Indonesia. Anthropogenic habitat alteration was defined as the clearing of forest for agriculture and small-scale forest product collection. Movement patterns, forest strata use, microhabitat use, and home range use were observed in two groups that occupied habitats with different levels of human alteration and where habitat quality was found to differ. The group occupying the heavily-altered habitat (Anca) spent a significantly greater proportion of time traveling on the ground than the group in minimally-altered habitat (CH), and significantly more time than expected in microhabitats within their range that were characterized by greater alteration (e.g., agroforestry areas). There was no significant difference between the two groups in daily path length, despite differences in group sizes. The Anca group exhibited a greater home range area per individual than the CH group, and utilized a more limited area within their home range with greater intensity, relative to the CH group. Tonkean macaques may therefore be responding to anthropogenic habitat alteration by adjusting their use of forest strata to facilitate travel and increase foraging opportunities, by intensively using particular areas within their home range where known resources are present and predictably available, but also by increasing their home range area per individual to cover more area and extending their overall search effort on a daily basis.

Keywords: flexibility; habitat use; ranging; Sulawesi macaque; habitat alteration

INTRODUCTION

The examination of the use of space is central to many socioecological studies of nonhuman primates because the efficient use of habitat contributes to their ability to survive and ultimately reproduce (Overdorff, 1996). The considerable variability in patterns of movement and use of space observed across the primate order is primarily explained by the distribution and availability of food resources (Clutton-Brock, 1977; Gautier-Hion et al., 1981; Kinnaird, 1990; O'Brien & Kinnaird, 1997; Oluput et al., 1997; Watts, 1998). In general, primates that exploit highly dispersed and unpredictable food sources (e.g., most fruits) tend to travel further each day and cover a larger area in the course of the year than species who feed on dense resources that are more evenly distributed and predictably available (Oates, 1987). Similarly, in seasonal environments, where there are periods of food scarcity, primates may travel more frequently and further during these times of reduced availability (Terborgh, 1983; Chapman, 1988a; Isbell & Young, 1993).

Anthropogenic habitat alteration, which often results in lower quality habitat characterized by a diminished food supply (Struhsaker, 1997), may also produce similar "resource-scarce" ecological conditions to which primates must respond in terms of ranging and habitat use. For example, for *Macaca nigra*, O'Brien & Kinnaird (1997) found that the group whose range included the least amount of primary forest traveled the farthest each day. Lee (1997) found, also for *M. nigra*, a significant negative correlation between basal area of trees within the home range and daily path length, suggesting that distance traveled is greater in habitats of lower quality. For Barbary macaques (*M. sylvanus*), Menard & Vallet (1997) found that a group in a habitat of poorer quality spent more time moving and had longer daily path lengths than a group in a resource rich site. Singh et al. (2001), however, found daily path lengths of groups of lion-tailed macaques (*M. silenus*) in forest fragments to be shorter than those of groups in continuous forest. The authors suggest that this finding might reflect the strategy of reducing energy and time expenditure in travel in habitats of lower quality. Home range size may also be affected by habitat quality, whereby groups living in habitats of lower resource availability may need to cover a larger area in order obtain sufficient nutrients (Chapman, 1988a; Wieczkowksi, in press).

Habitat disturbance and the concomitant reduction in habitat quality can also influence nonhuman primates' use of space (Gautier-Hion et al., 1981). When faced with a choice of microhabitat types within a home range, a primate group would be expected to prefer areas of intact, minimally-disturbed primary or old secondary forest where there is well developed canopy structure and where food resources are likely to be more abundant (Leighton, 1993; Heiduck, 2002). O'Brien and Kinnaird (1997), for example, found that crested black macaques showed a preference for primary forest within their range; areas where preferred strangling figs (e.g., *Ficus caulocarpa* and *Ficus benjamina*) and their preferred fruit species, *Dracontomelum dao*, were at the highest densities and where human disturbance was minimal. Use of forest strata may also be affected by changes in habitat. Singh et al. (2001) found a six-fold increase in time spent on the ground from 1990-1991 to 1999-2000 for lion-tailed macaques inhabiting a deteriorating rain forest fragment in Western Ghats, India. Finally, given that the use of space within a home range has been shown to be related to presence of preferred food trees (Oluput et al., 1997; O'Brien & Kinnaird, 1997), groups in heavily-altered habitats may show a less even use of space than groups in unaltered or less altered habitats because their foraging options are limited to what remains in the habitat.

The genus *Macaca*, which is the most widely distributed of the nonhuman primates, is broadly recognized for its great adaptability, showing significant ecological plasticity by occupying a diversity of habitats (Albrecht, 1978; Fooden, 1980; Fa, 1989). The oceanic island of Sulawesi hosts at least seven species of macaques, which amounts to approximately 37% of macaque species in only 1% of the geographical range of the genus (Fooden, 1969; Sugardjito et al., 1989). The ecological conditions of the Sulawesi macaques are distinct, compared to other Southeast Asian primates, in a number of parameters: they have no catarrhine primate competitors, except where they occur parapatrically in hybrid zones (Bynum et al. 1997a, 1997b); they have few "natural" predators (i.e., birds of prey, snakes, large cats); and their forests exhibit less floral diversity than other Southeast Asian forests (Whitmore & Sidiyasa, 1986). Although most behavioral information on Sulawesi macaques comes from studies on captive groups (e.g., Bernstein & Baker, 1988; Thierry 1984, 1985), the number of studies on wild populations has increased in the last two decades with long-term work conducted on *M. nigra* (Lee, 1997; O'Brien & Kinnaird, 1997; Rosenbaum et al., 1998), and *M. nigrescens* (Kohlhaas, 1993) in North Sulawesi. Two of the seven endemic species (*M. tonkeana* and *M. ochreata*), however, remain the subjects of only short term observations (e.g., Supriatna, 1991; Bynum, 1995; Kilner, 2001; Lennox, 2002).

In this paper, I investigate the flexibility in ranging patterns and use of habitat of the Sulawesi Tonkean macaque (*Macaca tonkeana*) in response to anthropogenic habitat alteration. Anthropogenic habitat alteration was defined as the clearance of forest for agriculture and small-scale forest product collection. I studied two groups that occupied habitats with different levels of alteration and where habitat quality was found to differ (Riley, in prep. a) in order to test several predictions regarding their movement patterns and use of space. The two groups also differed in size (i.e., 6-9 versus 27-28+ individuals), with the smaller group occupying the heavily-altered habitat (and the small size probably reflective of the diminished carrying capacity of the highly disturbed environment). The latter group's diet composition and activity patterns, important aspects of foraging efficiency, have been shown to reflect the nature of their habitat and the diminished resources available (Riley, in prep. a). The perspective taken here is to document whether this group's use of space is also part of a patterned response to its lower quality habitat. By contrasting this group's response to specifics of the quality and structure of its habitat with the pattern exhibited by a group less impacted by habitat alteration, a more comprehensive understanding of the ecological flexibility of Tonkean macaques can be achieved.

In general, time spent in different forest strata should be expected to be related to differences in habitat quality, with the group in the heavily-altered habitat expected to spend more time on the ground (i.e., because there are fewer trees available for foraging and travel). With regard to microhabitat use within their ranges, both groups were expected to spend more time in continuous forest areas than more altered microhabitats (e.g., agroforested areas) (especially because these areas tend to have greater fruit abundance due to a higher occurrence of mid-canopy and canopy-sized trees). If the smaller size of the group in the more altered habitat is associated with increased access to limited resources, then the expectation of greater daily path length and home range size for groups occupying heavily-altered habitat may not be supported. Intensity of range use, alternatively, may differ between groups, with the group living in heavily-altered habitat expected to use certain quadrats more intensively than others due to reduced abundance of food resources and a more patchy distribution of those resources across its range.

METHODS

Study site

The research was conducted in the Lake Lindu valley enclave, which is situated at approximately 1,000 m.a.s.l., in Lore Lindu National Park (01°15' to 01°30' S; 119°50' to 120°20' E) in Central Sulawesi, Indonesia from June 2002 - April 2004 (Riley, in prep. a). Details of the study site are reported elsewhere (Riley, in prep. a).

Study animals and habitat characteristics

Two groups of *M. tonkeana,* occupying habitats which differed in levels of anthropogenic alteration and overall quality, were studied (Table 3.1). The first group (hereafter, "Anca") occupied heavily-altered forest, characterized by frequent use by villagers (e.g., tree felling for livelihood needs) and conversion of forest to agricultural and agroforestry areas. The second group (hereafter, "CH") occupied minimally-altered forest (i.e., no agricultural areas, except for one coffee agroforest garden on the southwestern edge of the group's range, yet frequent collection of rattan) inside the boundary of the National Park. As reported elsewhere (Riley, in prep. a), habitat quality, defined in terms of specific measures of the abundance, productivity, and distribution of food resources, was found to be greater in the minimally-altered, CH habitat. Group sizes averaged 7.5 and 27 for the Anca and CH groups, respectively (Table 3.1).

Table 3.1. Group composition and habitat characteristics

Feature	Anca	CH
Group Size (range)	6-9	26-28+
Group Composition[a]	3M, 2F, 2SJ, 2I Changes: -1M, -2SJ, -1I	9M, 9F, 5LJ, 3SJ,1I, 1+U Changes: -1I, -1F
Habitat alteration[b]	Agroforestry (coffee, cacao) = 66% of group's range	One coffee agroforest garden at periphery of range = 2.1% of group's range

	Forest product collection (wood, rattan, wildlife)	Forest product collection (rattan)

[a] At maximum; M = adult male, F = adult female, LJ = large juvenile, SJ = small juvenile, I = infant, U = unknown.

[b] See Riley (in prep. a) for details of resultant variation in habitat quality.

Data collection

Habitat use

Prior to the start of systematic data collection, I habituated the two groups to the point of tolerating human presence at a distance of less than 10 m. I then collected data on each of the two groups for 3 consecutive days each month for 15 months, between January 2003 and April 2004 (see Riley, in prep a.). Following Kinnaird (1990), every half hour, 10 minutes were spent taking a scan sample (Martin & Bateson, 1993) of the group, recording the following information for each individual located: location in the forest strata (categories: 0m (on ground), >0-2m, >2-12m, >12-20m, and >20m), and microhabitat type. Microhabitat types were defined as: (1) continuous forest: forest bounded on =1 side by agroforestry/agricultural areas, (2) broken forest: forest areas separated from continuous forest on =2 sides by agricultural areas, and (3) forest garden: agricultural areas present within the forest. A total of 747 scans, over 373.5 hours across 45 days, were collected for the Anca group. For the CH group, 473 scans were collected during 236.5 hours across 36 days. During day follows, I also noted the time and location of intergroup encounters.

Ranging Patterns

For both groups, daily follows began at 0600 h, and concluded when the group settled in its sleeping tree, or when the group was lost and could not be relocated. Immediately following each 10-min scan sample described above, I estimated and plotted the center-of-mass of the study group on maps of its habitat at half-hour intervals. Daily path length (DPL) was calculated by summing the straight-line distances between half-hour center-of-mass locations during a single day (Altmann & Altmann, 1970). For the several occasions when the groups left the trail system and were lost for several hours, I measured the shortest distance between where the groups were before they were lost to where they were found again, and considered that to be the distance traveled. Daily path lengths were mapped on 41 days for the Anca group, and 26 days for the CH group.

Home range size was calculated in two ways. Overall home range was calculated by drawing a line around the outermost sightings of the group (including ad libitum observations) and counting the number of quadrats within the line (Altmann & Altmann, 1970; Lee, 1997). I also calculated annual home range by summing the number of quadrats entered during a 12-mo period. The latter home range estimate was calculated using all data on quadrat use encompassing 44 and 38 days for the Anca and CH groups, respectively. Because the groups were occasionally lost for several hours, the estimates of daily path length and home range size that I report are likely to be underestimates of the actual values for the study groups.

Data Analysis

For all statistical tests, results were considered significant at $P = .05$. To test for predicted differences between the groups in mean percent time spent in different forest strata I used one-way Analysis of Variance (ANOVA) tests with group (i.e., habitat) as the main effect. Arcsine transformations were performed on these proportional data to meet assumptions of normality and equal variances (Sokal & Rohlf, 1981). Because there were within-group and between-group differences in the total number of observations collected per day throughout the data collection period, I used the Weighted Least Squares (WLS) function in the ANOVA models, where the weighted variable was the total number of observations per sample day.

To determine whether the two groups spent significantly more time in continuous forest areas than expected I used a chi-square test. For each group, this test compared usage proportions with the expected number of entries based on the percentage of each microhabitat within each group's home range. The percentage of each microhabitat type was estimated by coding the points of all intersecting trails as one of the three microhabitat types defined above.

A difference in mean daily path length (DPL) was assessed using a two-tailed t-test. Spearman rank correlation tests were used to reveal any associations between daily movement patterns (DPL), and rainfall or temperature. I also used a Spearman rank correlation test to determine whether DPL was correlated with time spent on the ground. Because the groups differed in size, I divided the annual home range size by the mean number of individuals in the group to obtain an adjusted measure of range size: per capita area (PCA) within the home range (home range area per individual) (Terborgh, 1983).

To investigate variation in the intensity of use across the groups' home ranges, I tabulated the number of times each group entered each quadrat of their home range over the study period. I measured the diversity of quadrat use for each of the two groups using the Shannon-Weaver index (H'). The formula for the diversity index is:

$$H' = (N \log N - \sum n_i \log n_i) / N,$$

in which N is the total number of sightings, n_i is the number of sightings in q_i (quadrat i). The t-value ($t = H_1^{'} - H_2^{'}\ /^{'}\ v\ s_1^2 + s_2^2$) was then computed and compared to the critical value of Student's t to determine whether the diversity indices computed for each group were significantly different (Brower & Zar, 1984; Zar, 1996). I also examined intensity of quadrat use by calculating the percentage of total sightings recorded within each quadrat for the two groups, and then classifying these into five levels of intensity (< 1%, 1-2%, 2-3%, 3-4%, and >4%) in order to visually represent each group's use of space within their home range (Kinnaird, 1990). When home range data of neighboring groups were available, I estimated home range overlap between the study group and a neighboring group by counting the number of quadrats in the overlap area and dividing this number by the total number of quadrats within the study group's overall range.

RESULTS

Habitat use

Forest strata use

Figure 3.1 illustrates differential use of the forest strata by the two groups; the CH group spent 86% of its time in the two upper forest strata levels, with very little time spent at lower levels, while the Anca group divided its time across all levels. As predicted, the Anca group spent a significantly greater proportion of its time on the ground than the CH group ($F = 155.34$, $P < .001$; Fig. 3.1).

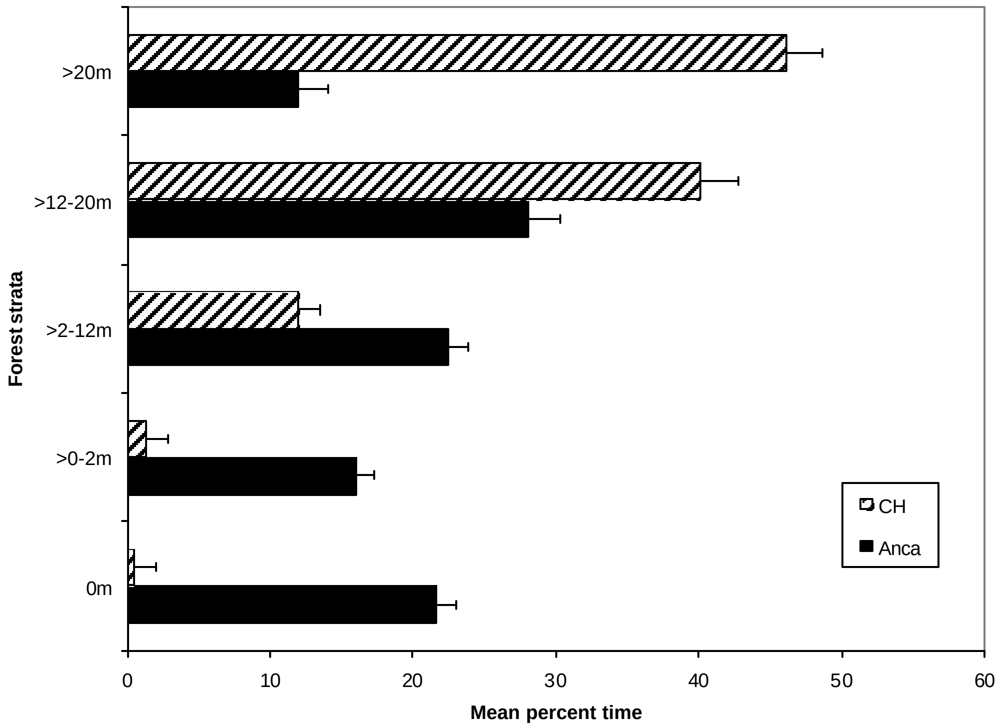
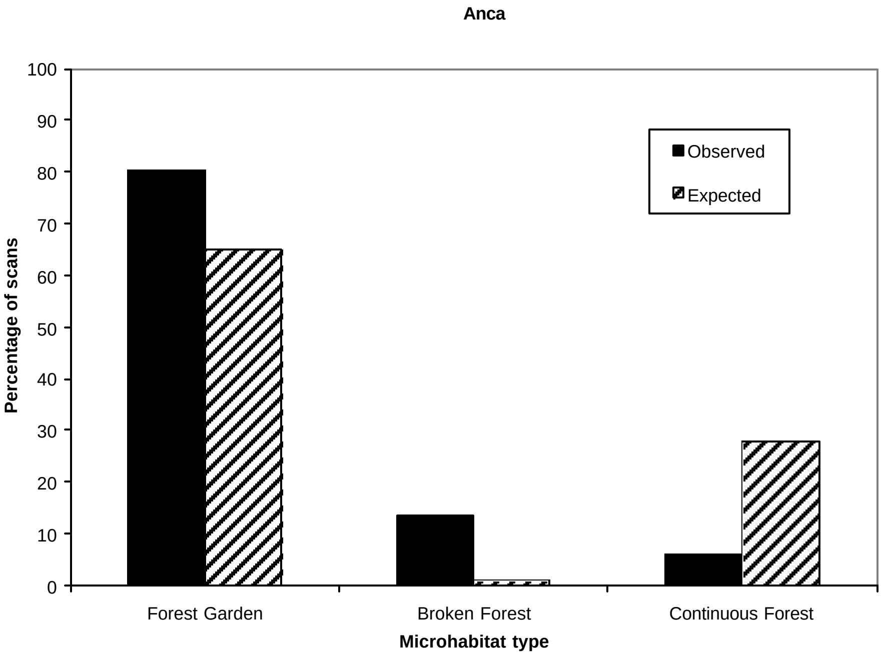


Figure 3.1. Mean percent time spent in different forest strata by the two groups. Error bars represent one standard error from the mean.

Microhabitat use

Chi-square tests comparing the observed frequency of microhabitat use with the expected frequency showed significant differences for both groups (Fig. 3.2). The Anca group spent more time in forest gardens than expected (based on the percent of each microhabitat type in the home range), more time in broken forest than expected, and less time in continuous forest than expected (Fig. 3.2; $?^2 = 6659.29$, df = 2, $P < .001$). The CH group spent less time in forest gardens and broken forest than expected, and more time in continuous forest than expected (Fig. 3.2; $?^2 = 413.07$, df = 2, $P < .001$).



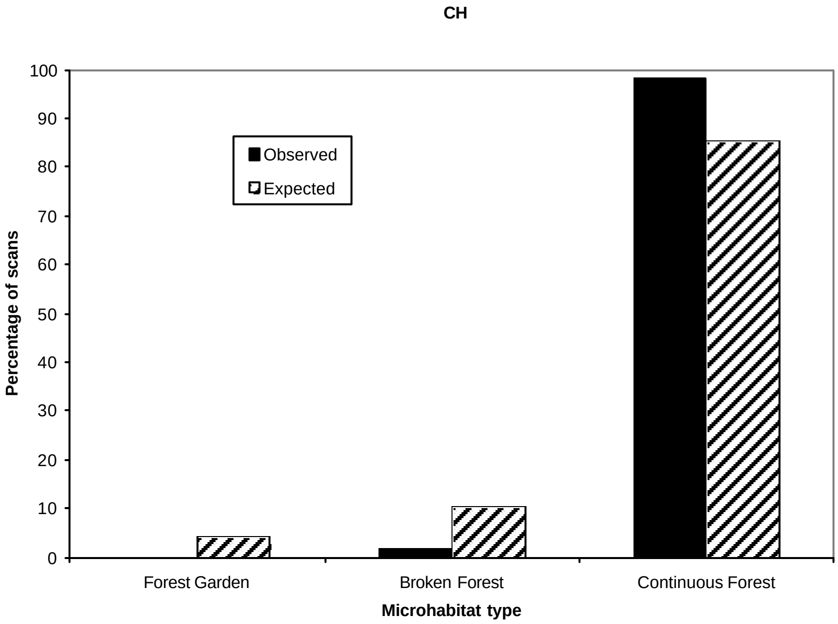


Figure 3.2. Percentage of scans in each microhabitat and expected observations based on the proportion of each microhabitat within each group's home range.

Ranging patterns

Movement

There was no significant difference in mean daily path length (t = 1.302, df = 65, *P* = .197) between the two groups (Table 3.2). Daily path length was not correlated with rainfall or temperature for either of the groups (Anca: rainfall, r_s = -.354, *P* = .215, temperature, r_s = .486, *P* = .329; CH: rainfall, r_s =.147, *P* = .615, temperature, r_s = -.321, *P* = .482). Daily path length was significantly correlated with mean percent time spent on the ground for the Anca group (r_s = .824, *P* <.001).

Table 3.2. Daily path length and home range for two study groups

Statistic	**Anca**	**CH**
Daily path length (m)		
Mean	1223.29	1098.31
SD	377.78	390.73
Overall home range (ha)	66.75	142.75
Home range (ha)		
12-month	35.25	72.5
Per capita area (PCA)	4.83	2.99

Home range size

During systematic behavioral observations, the Anca group was sighted in a total of 145 quadrats, while the CH group was sighted in 291 quadrats, representing annual home ranges of 35.25 ha and 72.5 ha for the Anca and CH groups, respectively (Table 3.2). Overall home range estimates, which included all ad libitum sightings of the two groups, increased these ranges to 66.75 ha (Anca) and 142.75 ha (CH). Although home range size was greater for the CH group, the group living in the heavily-altered habitat (Anca) had a greater home range area per individual (PCA) than the group in the minimally-altered habitat (CH) (Table 3.2).

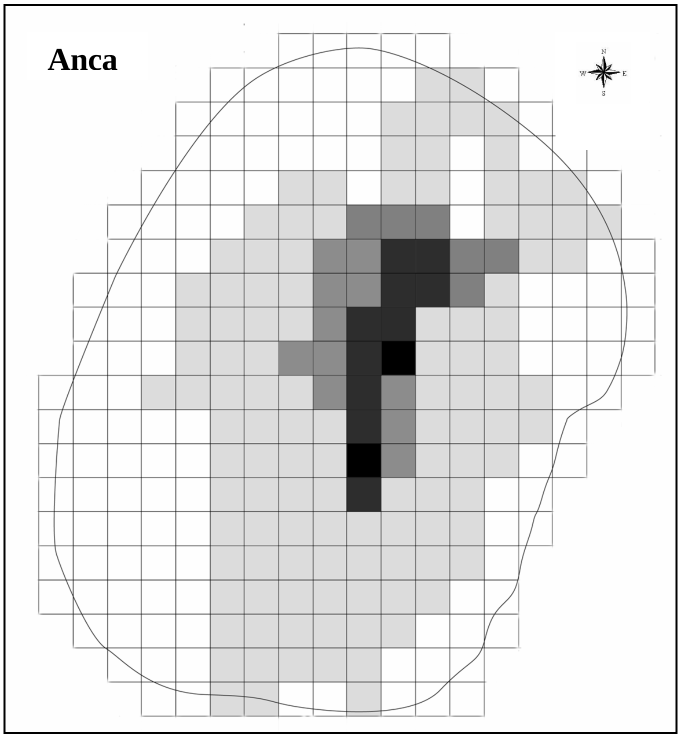
Patterns of home range use

The Anca group exhibited a significantly less diverse use of its home range than the CH group (Anca: H' = 1.77, CH: H' = 2.53; t = -50.25, df =1743, P <.0005); 50% of the Anca group's time was spent in only 27 quadrats (6.5 ha), versus 74 quadrats (18.5 ha) for the CH group. When mapped by levels of intensity of quadrat use (Fig. 3.3), the group differences in home range use were also apparent, with the Anca group utilizing a more limited area with greater intensity relative to the CH group. For both groups, however, almost half (A: 45.7%, CH: 49%) of the overall home range was not used during systematic behavioral observations. The Anca group returned to one of three specific sleeping trees (*Artocarpus teysmannii*, *Ficus pilosa*, and *Ficus* sp.) on 59% of the days in which their movement was measured. In contrast, the CH group never returned to any one sleeping tree during the course of the study.

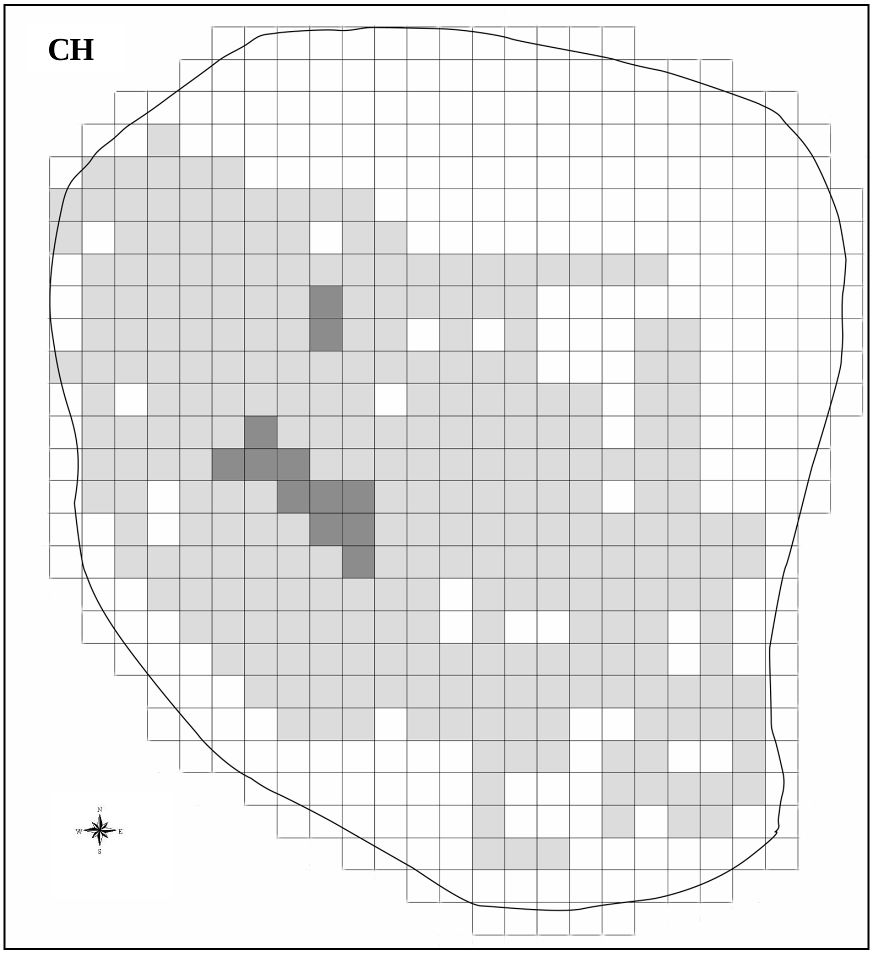
Intergroup encounters and home range overlap

I observed five intergroup encounters during day follows of the Anca group. On each of these occasions, the neighboring group was estimated to be larger in size (i.e., 15 + individuals). Three of these encounters occurred in agroforestry areas, one occurred in broken forest, and one occurred in continuous forest, within the Anca group's range. No intergroup encounters were observed during day follows of the CH group. Overlap in home range was observed between the CH group and a neighboring group (i.e., Kalora group), and was estimated to be 12% of the CH's overall home range.

Figure 3.3. Percent occupancy of each 0.25 ha quadrat in the two groups’ home ranges divided into five levels of intensity



■	3-4%
▩	2-3%
▨	1-2%
░	<1%
□	0%



DISCUSSION

Habitat use

Results from this study indicate that Tonkean macaques that live in heavily-altered forest spend a significantly greater proportion of time on the ground than those living in minimally-altered forest habitat. Menon & Poirier (1996) found a similar pattern in lion-tailed macaques (*M. silenus*); the group living in a forest fragment spent more time on the ground than groups living in protected forests. A significantly greater proportion of time spent on the ground may reflect the Anca group's need to adjust forest strata use in habitats where there are fewer large trees and significant forms of alteration (e.g., agricultural areas). This tendency towards terrestriality in disturbed habitats could also be related to rates of insect foraging and consumption (Lee, 1997), for the Anca group was found to supplement its diet with a higher intake of insects than the CH group (Riley, in prep a.). Post-hoc analysis of the frequency of insect consumption in different levels of forest strata, however, revealed that there was no significant difference in insect feeding frequency in lower versus upper levels of the forest strata for the Anca group ($?^2 = .014$. df = 1, $P = .906$).

Examination of forest strata use in heavily-altered areas is important with respect to allied concerns which can negatively impact populations of Tonkean macaques. The socioecological conditions of the Sulawesi macaques are considered distinct because there are fewer "natural" predators compared to other areas in Indonesia and Southeast Asia where macaques are found (van Schaik, 1989; Kohlhaas & Southwick, 1996). Humans, although not typically viewed as "natural predators," can also negatively impact primate population sizes and densities through hunting (Mittermeier, 1987; Peres, 2000), and hunting of macaques is a common practice in a number of areas in Lore Lindu National Park (Riley et al., 2000), despite the protected status of

Tonkean macaques. Villagers typically hunt macaques by setting up traps on the ground or by throwing rocks at solitary individuals which are then chased by dogs (Riley et al., 2000). Increased terrestriality of Tonkean macaques in human-modified habitats may therefore pose a threat to their survival. This may be the case even if hunting devices, such as traps, are not intended to capture macaques, as was evident in the present study when an approximately 20-month old juvenile from the Anca group was caught in a trap set for forest pigs within an agroforest area. On the other hand, travel through upper level forest strata in disturbed habitats, where canopy continuity has been lost and gaps are large, can result in an increased rate of falling (Singh et al., 2001). When faced with a significant loss of trees in their habitat, Tonkean macaques may be forced to travel more on the ground, as well as exploiting the resources available there, but these activities are not without risk.

Previous research with other Sulawesi macaques has indicated that groups whose ranges include a number of habitat types prefer primary forest to secondary forested areas (Lee, 1997). When examining habitats subject to extensive alteration, however, it is important to take into consideration what resources are available to groups in such environments and how those resources are distributed spatially across varying microhabitats. In this study, the Anca group spent more time in the agroforestry areas than was expected, which may reflect this group's reliance on food resources (e.g., *Arenga pinnata*, *Artocarpus spp.*, and *Ficus spp.)* that tend to be high in density in human-modified areas (Riley, in prep. a). More time than expected in agroforested areas may also be the result of the Anca group being attracted to cultivated foods within these areas. Although the Anca group did not raid cacao gardens, as did other groups in the park, they did frequently raid one specific papaya and banana garden (Riley, in prep. c). These patterns of microhabitat use may also result from the presence of neighboring groups, another factor known to restrict use of space and movement patterns in primates (Kinnaird, 1990; Ostro et al., 1999). Between-group encounters in the Anca group's range were most common on the borders of human-modified areas and continuous forest. By concentrating their activity in the agroforested areas, the Anca group may avoid encounters with larger neighboring groups which occupied areas of more continuous forest. This microhabitat may therefore represent space where they can efficiently use their energy; that is, to obtain nutrients without having to expend additional energy in the defense of the resources available.

Movement patterns and home range use

Movement patterns in primate groups have been shown to be influenced by climate (Menard & Vallet, 1997; Swedell, 2002), an effect that might be accentuated for groups occupying disturbed habitats (Lee, 1997). In this study, however, daily path length was not correlated with either rainfall or temperature, which suggests that other ecological variables may be more important determinants of movement patterns.

Lore Lindu National Park is not characterized by strong seasonal variation in rainfall and fruit production (Riley, in prep. a). Habitat alteration and the concomitant reduction in food supply may, however, be creating food-scarce conditions to which Tonkean macaques must respond. One response would be to increase daily path length and home range size in order to cover more area to obtain sufficient nutrients in a lower quality habitat (Chapman, 1988b). This expected response, however, makes assumptions about group size in relation to resource availability and distribution. If habitat quality and structure are held constant then group size will be expected to be an important factor influencing ranging and movement in primates, with larger groups exhibiting longer daily path lengths and larger home ranges (Waser, 1977; van Schaik et al., 1983; Isbell, 1991; Barton et al., 1992; Ostro et al., 1999). In heavily-altered environments, however, decreases in group size will reflect habitat quality, with smaller groups (or smaller foraging parties resulting from temporary fissioning) able to more efficiently utilize what resources are available. It is therefore possible that the small group size of the Anca group is the direct result of diminishing habitat quality affecting mortality or producing fission in a once larger group.

The much larger overall home range of the CH group (i.e., double the size of Anca's range) may reflect the larger group size for CH, or perhaps more appropriately, the smaller size of the Anca group. The equivalence between the two groups in daily path length, on the other hand, indicates that despite being significantly reduced in group size, the Anca group must still travel as far as a larger group in order to acquire necessary resources on a daily basis, given the overall lower resource availability in their habitat. This is also consistent with the larger areas utilized on an individual basis by Anca group members (PCA values) relative to CH individuals. Overall, these results suggest that in heavily-altered environments, decreased group size may permit a smaller overall home range, but the abundance and distribution of the limited resources may still require significant movement on a daily basis.

The most salient difference between groups living in heavily- versus minimally-altered habitats may have less to do with the amount of area they explore (daily and annually), than how they actually *use* the areas within their range (Ostro et al., 1999). The CH group, occupying minimally-altered habitat, showed an even use of its core range area. In contrast, the Anca group utilized a more limited area within its range with greater intensity. These findings may reflect the fact that key resources are more limited and spatially concentrated in the Anca group's habitat, while the CH group's range contains a greater number of resource options distributed throughout its range (Riley, in prep. a). For the Anca group, the quadrats used most intensively represented areas where consistently utilized and limited sleeping and food trees were located. Whereas the Anca group may forage over an extended area to acquire sufficient resources, they repeatedly returned to a small number of preferred sleeping trees. In contrast, the CH group never slept consecutively in the same tree, or even within the same quadrat throughout the duration of the study. Access to cultivated foods such as papaya and bananas, which are spatially concentrated and abundant at predictable times, may also have contributed to periodic intensified use of space for the Anca group, as has been shown in other studies (e.g., Brennan et al., 1985; Forthman-Quick, 1986; Saj et al., 1999).

Human-induced habitat alteration, which results in a reduction in tree abundance, key food species density, and levels of fruit production (Riley, in prep. a), appears to be an important influence on ranging patterns and habitat use in Tonkean macaques. Tonkean macaques may be responding to anthropogenic disturbance by adjusting their use of forest strata in order to facilitate travel and increase foraging opportunities, by intensively using particular areas within their home range where known resources are present and predictably available (e.g., *Arenga pinnata* palms), but also by increasing their home range size per individual to cover more area and extending their overall search effort on a daily basis. Whereas these assessments of the utilization of space suggest a capacity for Tonkean macaques to exhibit flexibility in their behavioral repertoire, signs of stress appear to be present (e.g., increased individual effort in acquiring resources, despite decreased group size) and survival may not be assured.

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CHAPTER 4

MY HABITAT OR THEIR HABITAT?: HUMAN-NONHUMAN PRIMATE OVERLAPPING RESOURCE USE IN LORE LINDU NATIONAL PARK, SULAWESI, INDONESIA[1]

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[1] Riley, E.P. To be submitted to *Conservation Biology*. This paper won the AAPA Primate Behavior and Biology Interest Group Student Award presentation at the 2005 annual meetings of American Association of Physical Anthropologists (AAPA).

ABSTRACT

The purpose of this study was to examine overlapping resource use by human and nonhuman primate (*Macaca tonkeana*) inhabitants of Lore Lindu National Park, Sulawesi, Indonesia. Methodology included (1) behavioral observations on two groups of macaques, (2) ethnographic interviews, (3) quantitative measurements of crop raiding in cacao (*Theobroma cacao*) gardens, and (4) phenological sampling of macaque forest foods. Seventeen plant species were utilized by both humans and the Tonkean macaques. Five of those species were among the top 10% of the most salient tree species listed by villagers, and constituted more than 80% of the macaque groups' diets. These results suggest that overlapping use of forest resources may have a serious impact on macaques living in human-modified environments, where habitat alteration is frequent. Although villagers considered the macaques the most destructive crop raiding animal, results from the garden surveys indicated that forest mice consumed a significantly greater number of cacao fruits than macaques. Crop raiding by macaques was not correlated with temporal patterns of forest fruit availability. In Lore Lindu National Park, where cacao gardens are subject to raiding by wildlife, the recommendation of encouraging shade cacao as a buffer zone crop adjacent to forest reserves may not be a suitable management tool. More appropriate management tools may be to encourage other shade-grown crops that are not raided by macaques (e.g., coffee), and to examine the role macaques play in the regeneration of forest tree species of economic and cultural significance for villagers. This research indicates that primate conservation efforts may require management strategies that incorporate research focused on the ecological and behavioral plasticity of nonhuman primates in human-modified landscapes, as well as research focused strongly on the sociocultural and economic realities of the people living in and relying on those same environments.

Key words: overlapping resource use, crop raiding, human-modified landscapes, conservation, *Macaca tonkeana*

INTRODUCTION

Since their proliferation within primatology in the 1960s, primate field studies have fundamentally been concerned with the behavior and ecology of nonhuman primates in their natural environments. There are, however, at least two interrelated problems associated with a reliance on an examination of the "natural context." First, in the changing contemporary world, it is becoming increasingly difficult to study a group of nonhuman primates that has not been subject to some form of human influence, whether through interaction, manipulation, or habitat alteration/destruction (Dolhinow & Fuentes 1999). The second problem concerns the actual existence of a "natural context," if "natural" is meant to imply a context which excludes humans. It is more likely that living in close proximity with other primates has characterized much of our evolutionary history, during which human primates and nonhuman primates competed, possibly directly and indirectly, for key resources in their shared environments for centuries, millennia, or possibly longer (Sponsel 1997; Sponsel et al. 2002; Sprague 2002). The potential longevity of this sympatry then begs the question of whether one or more forms of human-nonhuman primate symbiosis (i.e., commensalism, predation, parasitism, competition, mutualism, etc.) necessarily represent an unnatural situation (Gudger 1919; Southwick et al. 1965).

Rather than ignoring nonhuman primate populations that live in "unnatural" environments, a number of researchers have made it their explicit aim to explore the ways in which nonhuman primates respond to various aspects of human influence (Bishop et al. 1981). Richard et al. (1989), by analyzing feeding/foraging patterns of members of the genus *Macaca*, found that certain macaques have the ability to persist and even prosper in close proximity to human settlements. On the other hand, human proximity has been shown to have potentially negative demographic and socioecological consequences for nonhuman primates, such as, an increased likelihood of bi-directional disease transmission (Fa 1991; Engel-Jones 2001).

Human and nonhuman primates that are forced to live in ever-increasing proximity may also be more likely to experience conflict as each attempts to exploit common features of the environment (Hill, 2002). For example, at the Tana River Reserve in Kenya, Kinnaird (1992) found that the palm, *Phoenix reclinata*, is both heavily exploited by people of the Tana River District and provides an important food source for the endangered Tana River crested mangabey (*Cercocebus galeritus*). A number of the human uses of this palm are not sustainable, leading to habitat degradation and loss of an important resource (Kinnaird 1992). Overlapping use of this resource between villagers and the mangabeys therefore has negative consequences for the survival of the Tana mangabey.

The transformation of forests into agro-forested and agricultural lands can create new situations in which overlapping resource use can occur, given that such areas often result in the creation of new potential sources of food for nonhuman primates. Some primate species have adapted to such alterations in their environment by incorporating agricultural areas into their ecological repertoire (Wheatley 1980; Wada 1984; Eudey 1986; Richard et al. 1989; Supriatna et al. 1992; Hsu & Agoramoorthy 1997; Naughton-Treves 1997; Siex & Struhsaker 1999; Hill, 2000; Riley et al. 2000; Sprague 2002). These animals frequently raid agricultural areas and are subsequently deemed “pests” by human residents (Else 1991).

For nonhuman primates that inhabit forest-agriculture ecotones, agricultural crops may act as key food sources during periods of food scarcity in the forest. For example, Siex & Struhsaker (1999) found that Zanzibar red colobus monkeys consumed more cultivated coconuts when there were less wild foods available. Strum (1994) found that the most significant factor contributing to the development of crop raiding behavior in olive baboons was the reduction of natural forage available to them. This would suggest that the pressure to exploit cultivated foods may vary with seasonal availability of forest foods (Forthman-Quick 1986). In some cases, however, evidence for a relationship between wild food availability and the timing of crop raiding remains equivocal. Naughton-Treves et al. (1998), for example, found that crop raiding on maize by three primate species at Kibale National Park, Uganda was not related to forest fruit availability.

Although crop raiding constitutes an interesting example of primate ecological and behavioral flexibility, it may negatively affect the conservation norms of human communities living in proximity to forests. In many parts in Africa and Asia, for example, nonhuman primates are considered a threat to crops, and thus to human livelihoods, rather than a resource to be conserved (Hill 1997; Naughton-Treves 1997; Siex & Struhsaker 1999; Riley et al. 2000). The result is that cohabitation might be construed as beneficial, whereas in reality ecological flexibility may actually put the nonhuman primates in danger, as many farmers respond to crop raiding by trapping and/or shooting invading animals (Riley et al. 2000).

In this paper, I examine overlapping resource use by human and nonhuman primate (*Macaca tonkeana)* inhabitants of Lore Lindu National Park (LLNP), Central Sulawesi, Indonesia. I focus on both forest resources and human-created resources (i.e., cultivated foods). Specifically, I determined which forest resources are important for both macaques and humans and examine how the manner of human exploitation of these resources affects the potential use by macaques. To assess overlapping use of anthropogenic foods, I quantitatively measured macaque crop raiding on cacao tree crops (*Theobroma cacao*). I also assessed what ecological factors contribute to cacao crop vulnerability by testing the following hypotheses: (1) crop raiding is negatively correlated with forest fruit availability, and (2) cacao garden vulnerability is related to the distance of the garden from the village, and from forested area. Finally, I address questions concerning the implications of overlapping resource use for the future conservation of *M. tonkeana*.

METHODS

Study site

The research was conducted in the villages of Tomado and Anca in the Lake Lindu valley enclave in Lore Lindu National Park (01°15' to 01°30' S, 119°50' to 120°20' E) in Central Sulawesi, Indonesia (see Riley in prep. a). Lore Lindu National Park, comprising a total area of 217,982 ha, was established in 1993 from two existing reserves and is designated as a UNESCO Man and the Biosphere Reserve. In the Lindu valley, where the indigenous *To Lindu* (Kaili Tado') are predominantly wet-rice (*sawah*) farmers, it was not until the 1970s with the in-migration of Bugis people from South Sulawesi that cacao (*Theobroma cacao*) was introduced. In Indonesia, cacao is the third most important agricultural export, after rubber and palm oil (FAO 2003), supplying 14% of the world's cacao. Eighty-percent of Indonesia's supply is produced in Sulawesi. Cacao is a perennial crop that is typically cultivated under thinned primary-forest canopy, under regenerating forest after clear felling, or under the canopy of artificially planted trees (Greenberg 1998; N'goran 1998).

Study species

Macaca tonkeana, which is one of the seven macaque species endemic to Sulawesi, is among the least-known species on the island with regard to socioecology and conservation status (Bynum et al.1999). MacKinnon (1986) has suggested that although large reserves have been established in Central Sulawesi (e.g., Morowali and Lore Lindu), much of the area (i.e., lower to upper montane forest) within their boundaries may not be suitable habitat for *M. tonkeana*. The World Conservation Union (IUCN, 2004) currently lists *M. tonkeana* as "Lower Risk/Near Threatened" and Bynum et al. (1999) have proposed a total population estimate of 150,000 individuals (Bynum et al. 1999). As the threats of hunting (Lee 1999) and backlash on macaques due to crop raiding increase (Supriatna et al. 1992; Riley et al. 2000), however, the conservation status of *M. tonkeana* may require revision.

Data collection and analysis

Macaque forest resource use: diet composition

I collected data on the diet of *M. tonkeana* during systematic monthly observations of two groups from January 2003 to April 2004, as part of a study examining the impact of human-habitat alteration on the diet and activity patterns of Tonkean macaques (Riley in prep. a). The two social groups occupied habitats which differed in levels of human-induced habitat alteration: the "Anca" group occupied heavily-altered forest in the buffer zone, characterized by frequent use by villagers (e.g., tree felling for livelihood needs) and conversion of forest to agricultural and agroforestry areas. The second group, "CH," occupied minimally-altered forest (i.e., no agricultural areas, except one coffee agroforest garden on the southwestern edge of the group's range, yet frequent collection of rattan) inside the boundary of the National Park. Following Kinnaird (1990), every half hour, 10 minutes were spent taking a scan sample (Martin & Bateson, 1993) of the group. During each scan, if an individual was eating, I recorded the food item (e.g., young leaves, mature leaves, fruit (ripe or unripe), stems, shoots and sprouts, seeds, flowers, insects, and crops (type & part)), and species (Riley in prep. a). Supplemental data included ad libitum behavioral observations on two other groups of macaques ("WCS" and

"Kalora") living in human-altered areas, one of which ("Kalora") was known to raid cacao gardens.

Human forest resource use

I collected information on human forest resource use through personal observation and formal interviews with villagers (*n* = 45) from Anca and Tomado. Interview techniques included freelisting exercises and open-ended questions (Weller & Romney 1988). All interviews were conducted in Bahasa Indonesia by the author and then translated into English. For the freelisting exercises, I asked respondents to list all forest resources and tree species known to them. I then asked respondents to describe the purpose/function of each of the resources mentioned. The freelists were analyzed using ANTHROPAC 4.983 (Borgatti 2004) to determine which items were the most salient. Salience is a measure of how much knowledge respondents share and how important that knowledge is to them (Fleisher & Harrington 1998).

Crop raiding

To assess the extent and severity of crop raiding I collected three types of data. First, I conducted interviews with 11 cacao farmers in which I asked them to assess the frequency of crop raiding (i.e., never, occasionally, frequently, very frequently), and how crop-raiding affected their livelihoods. These farmers were selected because their gardens were in close proximity to a macaque group's range and/or known to suffer from crop damage by macaques. I also asked respondents from the human product forest use interviews to list all animals that raid crops. These freelists were then analyzed using ANTHROPAC 4.983 (Borgatti 2004) to determine which crop raiding animal was the most salient.

Second, I quantitatively measured the extent of crop loss caused by the macaques, as well as two other mammals (forest mice, Muridae, and forest squirrels, Sciuridae) known to raid cacao crops in 11 cacao gardens (Fig. 4.1). In each cacao garden, each cacao tree was counted, assigned a number, and the shade management system used in the garden was noted (Codes: 1 = Mix of thinned primary/older secondary forest with planted shade trees (*Erythrina* spp., *Musa* spp.), 2 = Planted shade trees with occasional remnant forest species, 3 = No shade, 4 = Little to no shade (a few remnant forest species present)). Every two weeks each garden was surveyed and the following information was recorded for each tree in the garden: (1) the number of fruits on the tree, and (2) the number of fruits eaten by macaques, the mouse, and the squirrel, based on the remains of consumed cacao fruits. After each survey, the remains of consumed cacao fruits were discarded so that they would not be counted again in the subsequent survey. Identification of the species responsible for the damage was possible because each species exploits the cacao fruit in a different manner: macaques rip the fruit off the tree, consume the flesh, and leave large chunks (golf-ball sized) of the rind; forest squirrels will also remove the fruit from the tree but the pieces that remain are small (i.e., size of a penny), while forest mice consume fruits that are still attached to the tree. Although cacao is a perennial tree crop and produces fruit year round, there is typically a fruiting season where peaks in cacao fruit abundance are observed. This represents the time during which farmers do most of their harvesting. Data were collected during the fruiting season of December 2002 to August 2003.

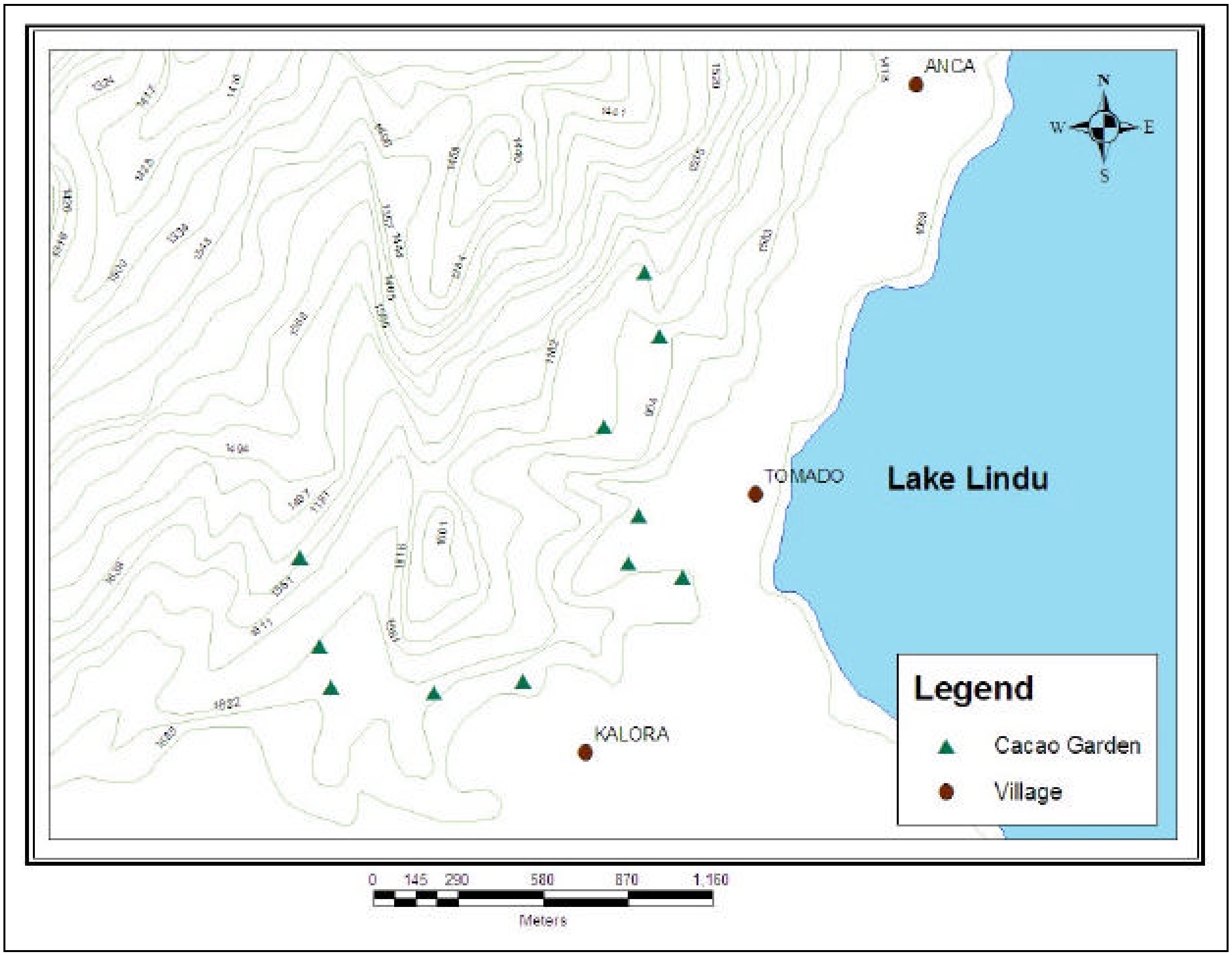

Fig. 4.1. Cacao gardens surveyed.

From these data, I calculated the percentage of fruit consumed per species per month by dividing the number of fruits eaten by each species by the number of available fruit from the previous survey. I then calculated the average percentage of fruit consumed by each species across the fruiting season. In addition, because the ultimate value of the cacao fruit for farmers is the number of kilograms of dried seeds they can sell, I also calculated the number of kilograms (using farmers' estimation of 25 fruits = 1 kilogram) lost due to crop raiding by each of the three mammal species. I used a two-tailed Friedman test to determine whether there were significant differences in total crop loss caused by the three species.

Third, to determine whether crop raiding is related to patterns of forest fruit availability, I collected phenological data from 10 vegetation plots (25 X 25 m) that were established within the home range of the Kalora group, a group known to raid cacao gardens. The ten phenology plots were chosen out of total of 40 plots established within this group's range because these plots contained the greatest number of macaque food species. In each plot all trees =20 cm diameter-at-breast height (DBH), all fig species (*Ficus*), and any other tree species known to be a macaque food item (based on preliminary observations and other studies of Sulawesi macaques) were enumerated, identified, and tagged. The phenological state of each tagged tree was estimated once a month on predetermined dates via visual examination with binoculars. Percentages of new leaves, flowering buds, flowers, unripe fruit, and ripe fruit were estimated (i.e., proportion of the total canopy covered by the item) and assigned an abundance score from 0-4, where 0 = 0% of the canopy, 1 = 1-25%, 2 = 26-50%, 3 = 51-75%, and 4 = 76-100%.

From these data I calculated a mean species abundance score for each tree species within the plots known to be a macaque food. These mean species abundance scores were then multiplied by the species density to derive a composite score. An index of total fruit availability was then derived by taking the sum of the composite species scores and dividing by the number of species in the sample (Wieczkowksi 2003). This index was calculated using ripe fruit abundance scores and lumped scores for ripe and unripe fruit. I tested for a significant negative correlation between forest fruit availability and the amount of cacao crop loss using the Spearman's rank correlation test.

To determine whether the location of the cacao garden was related to crop loss, I measured the distance from each of the gardens to the nearest forested area and to the closest village. I tested for a significant positive correlation between distance of the gardens from the village and the overall amount of crop loss using the Spearman's rank correlation test. If there was variability in the distance to forested area among the gardens, I tested for a significant negative correlation between distance to forested areas and amount of crop loss using the Spearman's rank correlation test. For all statistical tests, results were considered significant at $p = 0.05$.

RESULTS

Human and nonhuman primate forest resource use

A total of 20 forest resources were listed by the respondents. Table 4.1 indicates the top five most salient forest resources.

Table 4.1. Top five most salient forest resources for villagers

Forest resource	**Frequency**[a]	**Response %**[b]	**Average Rank**[c]	**Salience**
Rattan	43	96	1.442	0.820
Wood	29	64	2.034	0.436
Fruit	9	20	2.444	0.122
Tree resin	7	16	2.429	0.096
Arenga palm	9	20	3.333	0.088

[a] Number of freelists in which the item appears. [b] Percentage of respondents who listed the item.
[c] Average position in which the category appeared in freelists.

Seventeen plant species were utilized by both humans and the Tonkean macaques (Table 4.2). The most salient tree species for villagers, *Elmerillia ovalis,* constituted a small percentage of the macaque diet (Table 4.2 & 4.3). Five species, namely *Arenga pinnata*, *Elmerillia tsiampacca*, *Artocarpus teysmanii, Ficus* spp., and *Pandanus* spp., which were among the top 10% of the most salient tree species listed by respondents, constituted more than 80% of the macaque groups' diets (i.e., 82% and 85.6% for the Anca and CH groups, respectively) (Table 4.2 & 4.3). Rattan, which was the most salient forest resource listed by the respondents, only constituted a small proportion of the plant species diet for the two macaque groups (Table 4.1 &

4.2). Within the home range of the Anca group, 15 canopy-sized trees (i.e., two *Artocarpus teysmannii,* one *Elmerillia ovalis*, eight *Palaquium obovatum,* one *Dysoxylum densiflorum,* one *Rhus* cf. *taitensis*, and one *Lekotu)* were felled within the span of three months for the construction of dug-out canoes.

Table 4.2. Forest tree species used by both humans and macaques: parts used, specific uses, and percent contribution to macaque diet[a]

	Human	***Macaque***		
Species (Vernacular name)	**Part Used/ Specific Uses**	**Part Used**	**Diet: Anca**	**Diet : CH**
Arenga pinnata (Enau)	Leaves: thatching of roofs Palm fibers: brooms, thatched roofs Sap: *saguer* (fermented palm wine), *captikus* or *arak* (distilled palm wine), palm sugar Stem core: sago	Fruit	52%	1.3%
Artocarpus teysmannii (Tea)	Wood: dug-out canoes Sap: glue	Fruit	4.5%	0%
Ficus spp. (Beringin)	Firewood	Fruit Young leaves	21.9%	51.1%
Elmerillia ovalis (Uru)	Wood: lumber for house construction, dug-out canoes	Fruit	0.3%	*
Elmerillia tsiampacca (Takasa)	Wood: lumber for house construction, dug-out canoes	Fruit	2.8%	20.7%
Pinanga spp., *Areca vestiaria* (Pinang)	Fruit Trunk: roof and floor construction Apical bud: palm-cabbage	Fruit Palm cabbage New shoots	2.2%	4.1%
Calamus spp. & *Daemonorops* spp. (Rotan)	Parts used: leaves, stems, fruit Construction: roof, fences, small huts Furniture: chairs, tables, wardrobes	Stems Fruit New shoots	0.3%	0.6%

	Weaving: floor mats, baskets, fish baskets Shoots: food Sale: cash			
Lithocarpus spp. (Palili)	Bark: taste enhancer for palm wine	Fruit	*	-
Timonius teysmannii (Kalambio)	Fruit	Fruit	0.8%	-
Harpulia cupanioides (Sipu)	Fruit	Fruit[b]	-	-
Artocarpus vriescana (Baloli)	Fruit	Fruit	3.1%	-
Bruinsmia styracea (Kalia/Kompu)	Fruit	Fruit	2%	*
Villebrunea rubescens (Marangkapi)	Wood: construction	Flowers Young leaves	0.6%	-
Cratoxylon celebicum (Tomondu)	Fruit	Fruit	*	-
Pandanus spp. (Naso)	Leaves: floor mats, baskets	Fruit New shoots	0.8%	12.5%
Mangifera foetida (Mangga anca)	Fruit	Fruit	0.3%	-
Dysoxylum nutans (Langsat/lonca ibo)	Fruit	Fruit	0.3%	-

[a] Plant species diet. [b] Ad libitum observations on Kalora group. *Ad libitum observation. - Not observed

Table 4.3. Human saliency scores of tree species used by both humans and macaques

Tree Species	**Frequency**	**Response %**	**Average rank**	**Salience**	**Salience rank**[a]
Elmerillia ovalis	29	64	2.172	0.577	1
Ficus spp.	14	31	6.214	0.174	5
Elmerillia tsiampacca	7	16	5.429	0.102	9
Pandanus spp.	7	16	4.571	0.096	10
Artocarpus teysmannii	8	18	6.75	0.094	11
Arenga pinnata	9	20	7.444	0.084	12
Lithocarpus spp.	5	11	6.8	0.073	14
Mangifera foetida	4	9	6	0.043	24
Pinang palms	6	13	14.667	0.042	25
Artocarpus vriescana	4	9	16	0.030	34
Cratoxylon celebicum	4	9	18	0.025	42
Timonius teysmannii	2	4	20.5	0.020	48
Villebrunea rubescens	1	2	8	0.009	87
Harpulia cupanioides	2	4	24.5	0.009	85
Bruinsmia styracea	1	2	47	0.001	112

[a] Out of total species listed (*n* = 113)

Crop raiding

A total of 16 animals were listed as crop raiders by 35 respondents. Among the animals claimed to raid cacao crops, macaques were considered the most salient (Table 4.4).

Table 4.4. Saliency scores of cacao crop raiding animals

Crop raiding animal	**Frequency**	**Response %**	**Average rank**	**Salience**
Monkey	14	40	1.5	0.326
Forest mouse	16	46	2.188	0.288
Forest squirrel	12	34	2.75	0.183

Out of the 11 cacao gardens surveyed (Table 4.5, Fig. 4.2), three gardens (CG4, CG5, and CG6) were not subject to crop raiding by macaques, even though there was a macaque group whose range included these gardens. Table 4.6 shows farmers' assessments of the frequency of crop raiding and its impact on their livelihoods.

Table 4.5. Cacao gardens surveyed

Cacao garden	**Ethnicity of owner**	**Distance to village (m)**	**Total area of garden (ha)**	**No. of cacao trees**	**Shade management system**[a]
CG1	Toraja[b]	350m	+ 1 ha	547	2
CG2	Bugis				
#1		1225m	~ 1.5 ha	608	3
#2		1425m	~ 1.5 ha	394	3
CG3	Bugis	218m	1 ha	414	3
CG4	Bugis	600m	2 ha	303	4
CG5	Bugis	350m	5 ha	1902	4
CG6	Bugis	580m	3 ha	1215	4
CG7	Mandar	1325m	1 ha	300	3
CG8	Kaili Tado’	330m	1 ha	377	1
CG9	Kaili Moma’				
#1		383m	1 ha	124	3
#2		776m	1 ha	191	4

[a] Codes: 1 = Mix of thinned primary/older secondary forest with planted shade trees (*Erythrina* spp., *Musa* spp.), 2 = Planted shade trees with occasional remnant forest species, 3 = No shade, 4 = Little to no shade (a few remnant forest species present). [b] Married to a *To Lindu* woman.

Table 4.6. Assessments by farmers of frequency of macaque crop raiding and its impact on their livelihoods

Garden	Frequency of macaque crop raiding	Impact of crop raiding on livelihood
CG1	Rarely	"Macaques don't disturb the garden because it [garden] is located close to the village."
CG2	Very Frequently	"Macaques have entered the gardens and eaten the cacao fruit since 1985. In one month they will consume more than ¾ of the harvest."
CG3	Very Frequently	"75% of potential harvest is lost because of macaque crop raiding."
CG4	Never	
CG5	Never	
CG6	Never	
CG7	Frequently	"Because the macaques raid the cacao gardens, it would be better to cut all the cacao trees down and plant coffee."
CG8	Only 1 individual raids	
CG9	Frequently	"I get only ¾ of my harvest, because the other ¼ is taken by the monkeys." "I leave them bananas so that they [macaques] will be full, and won't eat the cacao fruit." "I feel like I can't be too angry at them [macaques] because they have to eat too."

The average percentage of fruit consumed by forest mice ranged between 2.8%-22.2% whereas the average percentage of fruit taken by macaques and forest squirrels ranged between 0% - 6.4% and 0.2% - 3.3%, respectively. Forest mice consumed a significantly greater number of cacao fruits than macaques and forest squirrels in all of the cacao gardens (Friedman test, $?^2 = 16.909$, $p <.001$; Table 4.7). There was no significant difference in the number of cacao fruits consumed between macaques and forest squirrels (Wilcoxon Signed Ranks test: Z = -.178, p = .859).

Table 4.7. A comparison of the number of kilograms lost to crop raiding and the total number of kilograms harvested by farmers

Cacao garden	**Macaque (kg)**	**Mouse (kg)**	**Squirrel (kg)**	**Fruit harvested[a] (kg)**
CG1	0.2	27.3	1.4	100
CG2 #1	20.7	91.6	6.6	630[b]
CG2 #2	24.4	71.5	0.9	
CG3	7.2	14.4	2	110
CG4	0	17	9.3	152
CG5	0	118.2	23.2	1500
CG6	0	68	43.1	1900
CG7	10.4	57.3	5.8	182
CG8	1.2	6.1	0.7	100
CG9 #1	1.1	4.5	0.3	400[b]
CG9 #2	2.2	24.4	1.2	

[a] As reported by the farmers; cumulative amount for fruiting season of Dec 2002 – August 2003.
[b] Cumulative harvest for 2 gardens.

There was no significant negative correlation between crop raiding and total forest fruit availability (Spearman correlation coefficient, ripe fruit: $r_s = .632$, $n = 5$, $p = .13$; ripe and unripe fruit: $r_s = .154$, $n = 5$, $p = .40$; Fig. 4.2).

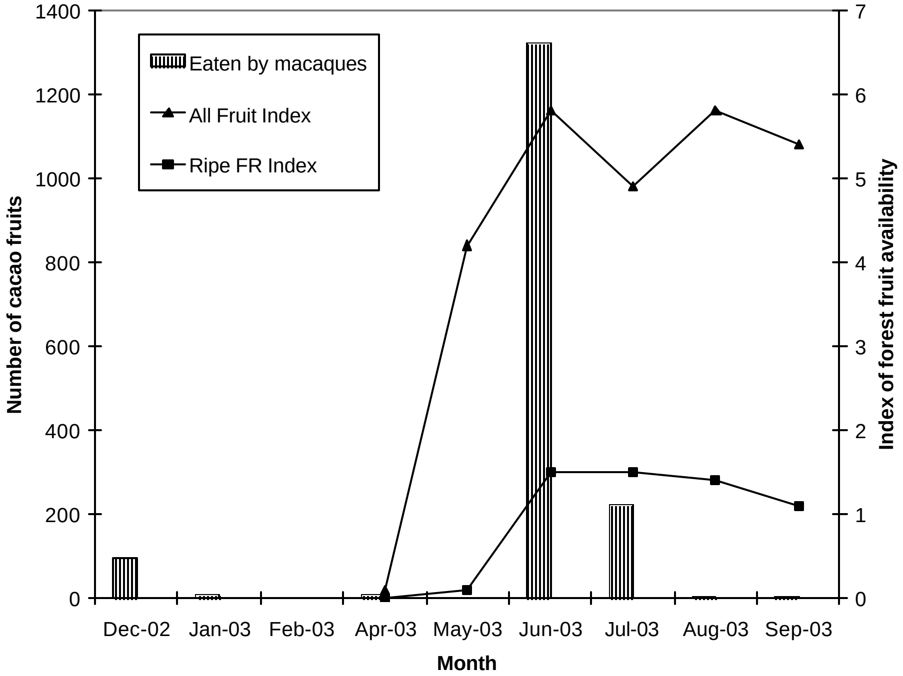

Figure 4.2. Temporal patterns of macaque crop raiding and forest fruit availability

The location of the cacao gardens in relation to the village was a reliable predictor of cacao crop loss; the greater the distance of the garden from the village, the greater the amount of cacao fruit consumed by the macaques (Spearman correlation coefficient, 1-tailed, $r_s = .714$, $n = 8$, $p = .023$).

DISCUSSION

The results indicate that there is considerable overlap in resource use between human and nonhuman primates for both wild and cultivated foods in the Lindu valley in Lore Lindu National Park.

Human and nonhuman primate forest resource use

Arenga pinnata, which is native to the Indo-Malayan archipelago and typically grows close to human settlements as well as in secondary lowland to hill forests, is regarded as one of the most important forest resources in the Asian humid tropics, including the Lindu valley, because of its remarkable versatility (Davis 1988; Mogea et al. 1991). Most products from the palm, such as the sap and hair fibers can be obtained without felling the tree. For example, the sap is tapped from male inflorescence stalks on the tree, and because there are many stalks on the palm, some may be fruiting (and thus provide a source of food for the macaques) while others may be tapped for the sap. Because the most important economic use of the palm is the inflorescence sap and the brown sugar that is obtained by boiling down the fresh juice, the palm is not usually felled (Davis 1988).

A. pinnata is also an extremely important resource for the macaques, with the fruit comprising more than 50% of plant food diet for the Anca group. For the CH group, which occupies minimally-disturbed forest, however, the palm only constituted a nominal percentage of their plant food diet. This discrepancy may reflect differences in the abundance and density of *Arenga pinnata* in the two groups' habitats; 8.8 trees/ha in Anca habitat compared to 0.4 trees/ha in the CH habitat (Riley in prep. a). These results suggest that *A. pinnata* may be particularly important for macaques living in heavily-altered habitats, such as the Anca group, where other important food resources may be less abundant due to pronounced anthropogenic habitat disturbance. Although there is overlap between humans and the macaques in the use of this resource, the manner in which villagers exploit the palm, which includes protection and cultivation, serves to ensure the persistence of the palm and thus may positively impact the ability of macaques to persist in human-modified landscapes.

Figs are widely recognized as keystone resources for many tropical frugivorous vertebrates because their fruiting patterns result in a reliable food source during times of general fruit scarcity (Leighton & Leighton 1983; Terborgh 1986). Kinnaird et al. (1999), based on research in Tangkoko Nature Reserve in North Sulawesi, contend that the genus *Ficus* is the single most important food source for Sulawesi's fruit-eating birds and mammals. The importance of *Ficus* to Tonkean macaques was also apparent in the research reported here, with figs constituting 21.9% and 51.1% to the plant species diets of the Anca and CH groups, respectively.

Fig trees are not removed from the CH group's habitat because of its location within the boundaries of the National Park. This likely explains why the density of strangling forms of *Ficus* is greater in CH habitat (33.2 individuals/ha) than in Anca (22.4 individuals/ha) (Riley in prep. a). This greater density of *Ficus* species also might account for why figs constitute the greatest proportion of the CH group diet. In Lindu, the felling of fig trees is not a common occurrence, even in permitted use areas, primarily due to folklore that contends that strangling figs are the home of an evil spirit. This folklore, however, seems to be losing validity among the Lindu; many villagers indicate that the predominance of religion (i.e., Christianity) now negates the belief in such evil spirits. This relaxing of a cultural taboo, in conjunction with the fact that many strangling figs grow on important lumber species (e.g., *Artocarpus teysmannii* and *Elmerillia tsiampacca*) that *are* felled, suggests that future human use may negatively affect the macaques ability to utilize this resource. This may be particularly dangerous for macaques in heavily-altered habitats, where they may be relying on *Ficus* spp. as keystone food resources.

Elmerillia tsiampacca constituted a much larger percentage of the plant species diet for the CH group, compared with the Anca group (20.7% and 2.8%, respectively). This difference might reflect, among other things (e.g., species density), that there is little overlapping use of this resource by humans and macaques in the CH habitat. The CH group's habitat is located within the boundaries of the National Park, more than 3 km from the villages, thus making the removal of this species impractical. In contrast, within the Anca group's habitat, this species is sought after for its strong wood for construction and dug-out canoes. In the Anca group's habitat, where density of *E. tsiampacca* is currently less than in CH habitat (CH: 2.4 trees/ha, Anca: 2 trees/ha; Riley in prep. a), and which experiences frequent forest use and conversion to agricultural land, any future human use of this resource may seriously impinge upon the survival of the Anca group.

In Indonesia, rattan is one of the most important forest products for both subsistence purposes and for its commercial market value (Weinstock 1983). Rattan is used to make furniture, and a variety of containers, from baskets to suitcases; it can be twisted for ropes, used for roofing, and the heart of the palm can be eaten (Weinstock 1983; Veevers-Carter 1984). For villagers of Lindu, rattan is regarded as the most important forest resource. The indigenous *To Lindu* collect rattan solely for daily household needs. Migrants, however, are extremely active in the collection of rattan for sale, particularly while awaiting wet-rice (*sawah*) harvest season and prior to major religious events/feasts (e.g., Ramadan and Christmas). For the Tonkean macaques, rattan constitutes a small proportion of their plant species diet, and therefore the collection of rattan does not appear to directly affect them. These results are similar to those found for two other Sulawesi macaques, *M. nigra* (O'Brien & Kinnaird 1997; Rosenbaum et al. 1998), and *M. nigrescens* in North Sulawesi (Kohlhaas 1993).

Overall, the results suggest that overlapping forest resource use may have a serious impact on macaque groups living in human-modified environments. Human use can include both clearing the forest for agriculture, which results in lower density of key macaque food trees and a less productive environment (Riley in prep. a), and selective removal of particular tree species for lumber. In Lindu, the latter practice tends to be conducted (on species such as *Elmerillia* *tsiampacca* and *Elmerillia ovalis*) when a village has plans to begin a major construction (e.g., in Tomado, a new laboratory was built for the elementary school, and a new church is in the process of being built). An exception to this, however, was observed in the beginning of 2003, where a major shift in the primary source of subsistence from farming to fishing throughout many of the villages in Lindu resulted in the felling of large old-growth hardwood species for dug-out canoes. Within the span of 3 months, 15 canopy-sized trees were felled in the already disturbed forest adjacent to the village of Anca for the sole purpose of constructing dug-out canoes. All of these trees were located in the core area of the Anca group. Three of those trees were known to be specific food trees for the Anca group, while the rest (particularly, *Palaquium obovatum*) provided other resources for the macaques, such as canopy connectivity and strata for resting and foraging.

Human and nonhuman primate use of cultivated resources

Previous ethnographic research with farmers in Lindu (Riley et al. 2000) indicated that many cacao farmers have a negative opinion of *M. tonkeana* because they contend that this primate consumes most of their crops' yields. Similar results were found in the present study; villagers list the macaques as the most destructive cacao crop raiding animal, and contend that the macaques negatively affect their livelihoods. The results from the cacao garden surveys, however, indicate that the amount of cacao fruit lost due to consumption by macaques is nominal when compared to the amount consumed by forest mice, and especially in relation to the amount of fruit still available for harvesting. Furthermore, not all macaques raid cacao gardens; neither the WCS group or the Anca group was observed raiding cacao, despite the presence of many cacao gardens within their ranges. Lindu farmers explain this difference as "those monkeys have just not learned yet."

Some studies have shown that primate crop raiding is related to patterns of forest fruit availability (Strum 1994; Siex & Struhsaker 1999). In this study, I found that macaques consumed cacao fruits regardless of levels of forest fruit abundance. This lack of support for a strong relationship suggests that one potential mechanism for alleviating crop loss (i.e., deliberate protection of particular wild foods known to be important food resources) may not be effective. For example, Naughton-Treves et al. (1998) were able to recommend deliberate management of *Mimusups bagshawei* as a means to alleviate crop raiding because they found that raiding of banana trees declined with increases in the availability of the fruit of this species. It should be acknowledged, however, that the phenology data for a number of the now discerned important macaque diet species are incomplete. The larger study which incorporates the research reported here was the first to systematically assess the diet of *M. tonkeana* and the phenology plots were established before a full year's cycle of diet data was completed. Resources now known to be especially important for the macaques (e.g., *Artocarpus teysmanii*, *Elmerillia tsiampacca*, *Arenga pinnata*, *Pandanus sp.*, *Ficus benjamina*, other *Ficus* spp., *Eleaocarpus musseri*; Riley in prep. a) could be incorporated into future research on the relationship between crop raiding and forest fruit availability, and the simultaneous sampling of cacao gardens and phenology should occur over a longer period of time.

Conservation implications of overlapping resource use

Given the overlap in resource use observed between the Tonkean macaques and villagers in Lindu, the ultimate question becomes: is cohabitation possible? Current approaches to conservation focus primarily on the protection of "biodiversity hotspots," areas of the highest levels of endemism and species diversity (Myers et al. 2000). Given the realization that only a small amount of forested area actually falls within protected areas (i.e., 12 % of Earth's land surface: Chape et al., 2005), more and more attention is being paid to the conservation value of lands outside of protected areas, such as human-modified habitats, and in particular agroforestry systems (Pimentel et al. 1992; Estrada & Coates-Estrada 1997; Greenberg 1998; Moguel & Toledo 1999; Petit & Petit 2003; Donald 2004). Such efforts are particularly relevant for wildlife, such as macaques, that do not recognize park boundaries and often utilize buffer zones that border protected areas (Salafsky 1993; Naughton-Treves et al. 2003).

Despite the fact that the planting of cacao (*Theobroma cacao*) has resulted in a considerable amount of deforestation in the humid tropics, cacao that is cultivated using a traditional forest farming system (i.e., crops grown under shade trees) is considered environmentally preferable to other forms of agriculture, such as those that require extensive clearing of forested areas (Donald 2004). High tree species diversity and multilayered forest structure of traditional forest farming systems serve to preserve many ecosystem functions and processes, such as maintaining soil organic matter levels, retaining soil productivity, decreasing run-off and soil loss, increasing foraging and nesting opportunities for birds, and providing connectivity between isolated primary forest fragments (Beer et al. 1998; Greenberg 1998; Siebert 2002; Donald 2004). Others, however, caution against an across-the-board adherence to such an approach, arguing that the conservation value of such systems depends on the type of shade management system in place (Rappole et al. 2003; Waltert 2004), and that the promotion of shade-systems may create an incentive to further convert areas of primary forest (Rappole et al. 2003). Moreover, because source habitats are defined by demographic characteristics (e.g., habitat-specific reproductive success and survivorship) rather than population density (Meffe & Carroll 1997), others caution against interpreting species richness to be an indicator of population viability when it may actually indicate the presence of a population sink (i.e., birth rate is generally lower than death rate) (Pulliam 1988; Waltert 2004).

An important component of the "cacao for conservation" argument, though, is the availability of a dense and diverse shade-tree assemblage, comprised primarily by natural shade trees (Greenberg et al. 2000). In Lindu, at least among migrants who possess the majority of the cacao gardens in Lindu, most of the cacao gardens surveyed exhibited little to no use of shade management systems. This choice of full sun production systems likely reflects the farmers' desire to increase yields—the viability of which, in the long-term, may be precarious, as witnessed in Malaysia where the cacao industry collapsed (Chok 1998; Donald 2004). Furthermore, in Lore Lindu National Park, where cacao gardens are subject to raiding by wildlife, the recommendation of encouraging shade cacao as a buffer zone crop adjacent to forest reserves (Greenberg 1998) may not be a suitable management tool. In addition, multiple-use areas, such as agroforests, may not be a viable primate conservation strategy where hunting occurs (Naughton-Treves et al. 2003). In Lindu, despite the fact that many macaques are crop raiders, the indigenous *To Lindu* do not hunt them. Opportunistic hunting of macaques does occur, however, among migrants who live near the village of Anca (Riley, unpublished data).

In places like Lindu, a more appropriate management strategy may be to explore ways to increase local tolerance to macaque crop raiding (Naughton-Treves et al. 1998). An important goal of this research was to communicate the results back to the farmers. This was accomplished through meetings with cacao farmers and other village officials, which entailed an initiation of discussion among participants about the reported findings. Many of the villagers present were surprised to learn that the macaques were responsible for a relatively nominal amount of cacao crop loss. A number of those present agreed that the amount lost to macaques is tolerable when viewed in comparison to the actual amount harvested. This acceptance may stem from a belief held by many in Lindu that the forests also belong to the macaques:

> I pity them [macaques] as they, too, need to find food. (*To Lindu* cacao and coffee farmer)
>
> I give them [macaques] a portion of my harvest, for they are looking for food too, they are hungry too. (*To Lindu* farmer)

Discussions also included a consideration of the best ways to guard the cacao gardens, such as knowing when macaques are more likely to enter (i.e., the data from behavioral observations suggest early morning and before dusk), keeping the gardens clean and well-cared for, burning fires to deter crop raiders, and learning from fellow farmers any innovative techniques to deter crop raiders (such as loud sound-making devices made from bamboo and traps set for forest mice). An important outcome of this meeting was the sense that there is now potential for farmers and other villagers to see the macaques in a more positive light, as perhaps a unique species of Sulawesi worthy of protection, rather than a major threat to their livelihoods.

Another approach to increasing local tolerance to human-macaque conflict is to explore the role of macaques in the regeneration of forest species that have economic and cultural significance for villagers. For example, Lambert (1998) found that a large percentage of plant species that have value to Ugandans at Kibale National Park are dispersed by a number of the frugivorous primates in the park. This finding suggests that maintaining populations of primates is important for human habitat use, and thus, provides a strong argument for their protection. The oceanic island of Sulawesi has relatively impoverished mammalian fauna due to historical biogeography (Lucas & Corlett 1998), and it may well be that the Sulawesi macaques act as major dispersal agents for plant species that are important forest resources for humans.

Results from this study also point to another potential management strategy of discouraging additional planting of cacao in areas close to the forest edge and far (>500m) from the village, and instead encouraging more shade coffee in lieu of cacao. Shade coffee (*Coffea arabica* and *C. robusta*) has been proposed as one of the most desirable land uses for buffer zones around protected areas (Petit & Petit 2003), not only for bird populations but for primate populations as well. For example, McCann et al. (2003) found that howler monkeys in Mombacho, Costa Rica rely on trees in areas of active shade coffee cultivation for food, travel, and rest, suggesting that shade coffee plantations serve as a vital refuge for howlers in Mombacho. Furthermore, appeal to the ever-growing market for products with low environmental impact (i.e., "green markets") can provide an incentive for farmers to enhance and protect traditional coffee production methods (Greenberg 1998; Albertin & Nair 2004). In Lindu, coffee is the second most important crop for villagers, both indigenous *To Lindu* and migrants, next to wet-rice agriculture (*sawah*). In contrast to their consumption of cacao fruit, macaques do not raid coffee plants, making this tree crop potentially more productive than cacao for farmers in Lindu. One obstacle to the promotion of a change in land management strategy emphasizing coffee over cacao, however, is economic (Estrada & Coates-Estrada 1997); harvesting costs may be greater for coffee than cacao, and the price of coffee in Indonesia has been extremely low in the last few years (i.e., 75% the price of cacao), making an emphasis on coffee much less desirable.

In the tropics, as human settlements grow and more forest is cleared for agriculture, often encroaching upon protected forest habitats for primates, human-nonhuman primate conflict over resources is a growing problem in primate conservation. Because such conflict may negatively affect the ecology and survival of nonhuman primates, and the conservation norms of local communities that live in proximity to forests, efforts directed at the long-term conservation of primates may be strongly dependent on effective management of the agriculture-forest ecotone

(Siex & Struhsaker 1999). Such efforts require integrative management strategies that incorporate research focused on the ecological and behavioral plasticity of nonhuman primates that use human-modified landscapes, as well as research focused strongly on the sociocultural and economic realities of the people living in and relying on those same environments.

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CHAPTER 5

CONCEPTUALIZING FORESTS, MONKEYS, AND PROTECTED AREAS IN THE LINDU VALLEY: IMPLICATIONS FOR CONSERVATION IN SULAWESI, INDONESIA[1]

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[1] Riley, E.P. To be submitted to *Human Ecology*.

ABSTRACT

The emerging field of ethnoprimatology investigates the ecological and cultural interconnections between human and nonhuman primates and their implications for conservation. In this paper, using an ethnoprimatological approach, I assess how local human ecology affects the conservation of the Sulawesi Tonkean macaque, *Macaca tonkeana*, in the Lindu valley of Lore Lindu National Park, Sulawesi, Indonesia. Information on local perceptions of the park and conservation, and how the Tonkean macaque is situated in local folklore was collected using formal and informal ethnographic interview techniques. Considerable diversity was found between the indigenous Lindu and migrants in knowledge, attitudes, and perceptions of the forest and its conservation. Only the Lindu possess folklore that envisions monkeys and humans as interrelated biologically, ecologically, and culturally. The significance of these findings is discussed with regard to the conservation of Tonkean macaques in areas of human-nonhuman primate overlap and the development of locally-based, collaborative conservation initiatives.

Keywords: ethnoprimatology; folklore; conservation; Sulawesi macaque; Indonesia

INTRODUCTION

The World Conservation Union (IUCN, 2004) has estimated that more than half of the world's nonhuman primates are of serious conservation concern, with 23% of them being listed as "Endangered" or "Critically Endangered." Ninety percent of all primate species are found in tropical forests, environments that are being converted to human use faster than any other habitats on earth (Mittermeier & Cheney, 1987). Throughout much of the 20th century, efforts to preserve these tropical forests and the wildlife that depend on them have been centered on the western-based idea of a protected area, in which forms of human intervention, such as settlement, and subsistence and commercial uses are prohibited (Stevens, 1997; Neumann, 1998). These tropical areas that provide habitats to most nonhuman primates, however, are found primarily in countries whose cultural, political, and economic realities often differ from those of foreign conservationists interested in developing and implementing conservation and management policies (Strum, 1986). Rather than being areas of "unspoiled wilderness," many protected areas have been created out of lands with long histories of human occupancy and use (Neumann, 1998). The establishment of National Parks and other protected areas is therefore often locally viewed as an act that has essentially criminalized customary land and natural resources uses for many communities across Africa and Southeast Asia (Ghimire, 1994; Vandergeest, 1996; Stevens, 1997; Neumann, 1998). Moreover, the restricted use/access policies that accompany the establishment of protected areas have resulted in many of these areas becoming arenas for struggles over resources between local residents, state conservation agencies, and international NGOs.

Beginning in the 1980s and increasingly in the last decade, the international conservation movement has begun to place less and less emphasis on the traditional model of human exclusion, recognizing that protected areas need to be managed within a broader ecological framework that includes the cooperation and support of local people (Brandon & Wells, 1992; Wells & McShane, 2004). Anthropologists, and other social scientists, have contributed to this movement by bringing to the forefront their insight into patterns of human behavior; that is, environmental ideologies and decision-making that encourage or impede conservation efforts (Orlove & Brush, 1996; Mascia et al., 2003). Within the discipline of anthropology specifically, a number of researchers have used an ethnoecological approach (Conklin, 1954) to reach an "understanding of local understanding" (Nazarea et al., 1998: 160) regarding natural resources and their management. For example, Nazarea et al. (1998) used an applied ethnoecological approach to ascertain culturally relevant indicators of sustainability and quality of life in Bukidnon, Philippines. An important finding of this research, as well as other studies conducted by social scientists that examine local attitudes towards conservation and the cultural, social, and ecological factors that shape those attitudes (e.g., Weber, 1987; Infield, 1988; Ellen, 1993; Newmark et al., 1993; Durbin & Ralambo, 1994; Mkanda & Munthali, 1994; Fiallo & Jacobson, 1995; Nepal & Weber, 1995; Boonzaier, 1996; Ite, 1996; deBoer & Baquete, 1998; Walpole & Goodwin, 2001; Kuriyan, 2002), is that people who live adjacent to protected areas often do not share the same perceptions of natural resources and conservation values as western conservationists. For example, Casagrande (2004), who studied Tzeltal Maya conceptions of primary forest, suggests that an exclusive focus on the scientific constructions of primary forest may not be productive because its importance is not appreciated by the local community. Kottak & Costa (1993) argue that in Madagascar, the economic value of forest (e.g., watershed protection) is a much more powerful incentive against forest degradation than are global goals like "preserving biodiversity" or lemur conservation.

Anthropological primatology has also contributed to this movement with a new approach, ethnoprimatology, which moves beyond the traditional boundaries of the science of primatology, ethnography, and conservation, and treats these fields as a unified area of investigation (Fuentes & Wolfe, 2002). Ethnoprimatology addresses the ecological and cultural interconnections between human and nonhuman primates, and the implications these interconnections have for conservation (Sponsel, 1997; Fuentes & Wolfe, 2002). A key feature of this approach is abandoning the idea of a pristine environment, and instead, envisioning humans and nonhuman primates as members of a dynamic ecosystem. Ethnoprimatology investigates, for example, how human and nonhuman primates are linked via central elements of the human primates' culture by elucidating the social and mythological relationships between humans and nonhuman primates. In some environments, these cultural conceptions may hinder primate conservation. For example, nonhuman primates represent an important source of food in many areas of South America and in Central and West Africa. Shepard (2002), in his research with the Matsigenka people in Manu National Park in Peru, identified how culture contact, changing resource use practices, and demography are affecting the way the Matsigenka subsist—changes that are now negatively affecting the monkeys in the region. The author suggests that as the human population grows, and as indigenous populations both inside and outside Manu gain greater access to Western goods and services, community-based management of hunting and resource use will become increasingly important. The indigenous Bari of Venezuela, whose view of the origin of monkeys is rooted in their mythology, hunt monkeys for food and for their teeth, which are prized for Bari necklaces, and capture them to use them as pets (Lizarralde, 2002). Changing ecologies, economies, and political realities for the Bari (e.g., increase population size, changing settlement patterns, and uses of technology) have resulted in declines in the primate populations in the area (Lizarralde, 2002).

Human-nonhuman primate cultural conceptions can also contribute to primate conservation. Cormier (2002) found that monkeys are central to the way of life in the material, social, and ideological aspects of the Guajá culture in western Maranhão, Brazil. Although the Guajá hunt primates for food and capture them for pets, Cormier (1999, 2002) found that sustainable hunting practices and the provision of refuges from habitat destruction contribute to primate conservation in the area. Asia is often considered the model of cultural tolerance of wild primates (Chapple, 1993; Knight, 1999). Among Hindus in India and Bali, monkeys hold a sacred status and therefore are tolerated and are not harmed by humans (Wheatley & Harya Putra, 1995; Carter & Carter, 1999). Buddhism, because in one of his reincarnations the Buddha was supposed to have been a monkey (Chapple, 1993), has also been credited with promoting tolerance and conservation of macaques in China and Thailand (Eudey, 1994; Zhao, 1994).

In this paper, I present research that utilized an ethnoprimatological approach to assess how local human ecology affects the conservation of the Tonkean macaque, *Macaca tonkeana,* in Lore Lindu National Park, Sulawesi, Indonesia. I broadly define human ecology as the ways in which people interact, both conceptually and actively, with their environment. The conceptual realm of human ecology is the focus here, examining (1) local perceptions of the National Park and conservation, and (2) how the Tonkean macaque is situated in local folklore, in order to assess how conceptualizations of the environment contribute to or impede conservation.

RESEARCH SETTING

The research was conducted in the villages of Tomado and Anca in the Lake Lindu valley enclave in Lore Lindu National Park (01°15' to 01°30' S, 119°50' to 120°20' E), Central Sulawesi, Indonesia (see Riley, in prep. a). Indonesia, the world's largest island complex, is home to at least 35 species of nonhuman primates (IUCN, 2004), 19 of which are island endemics (MacKinnon, 1987). On the island of Sulawesi, although only two primate genera (*Macaca* and *Tarsius*) are represented, the diversity within *Macaca* is considerable, with at least seven distinct endemic taxa (Bynum et al., 1999). The Sulawesi Tonkean macaque (*Macaca tonkeana)*, which is currently listed as “Lower Risk/Near Threatened” (IUCN, 2004), is actually among the least-well known on the island with regard to socioecology and conservation status because observational studies on the species have yet to exceed three months in duration (Bynum et al., 1999).

Indonesia is also one of the most ethnically and culturally heterogeneous nations; there are over 200 ethno-linguistic groups, 88% of which share the religion of Islam (Hugo 1992). The main threat facing Indonesia's nonhuman primates is the loss of habitat resulting from forest clearance for agriculture and logging (MacKinnon, 1987; Bynum et al., 1999). These activities are exacerbated by a large and rapidly expanding human population, reaching over 200 million in the 2000 census (FAOSTAT, 2004).

Lore Lindu National Park, comprising a total area of 217,982 ha, was established in 1993 from two existing reserves and is designated as a UNESCO Man and the Biosphere Reserve (TNC, 2001). The current indigenous ethnic groups around and within the park area are descended from migrations into the area around 4, 000 years ago (TNC, 2001). The northwest part of the National Park, where the Lindu valley is located, is primarily occupied by the Kaili people (TNC, 2001). Dutch conquest of the Kaili hinterland began in 1902, and in the Lindu valley resulted in the concentration of hill farmers into three settlements (i.e., Anca, Tomado, and Langko) along the lakeside (Acciaioli, 1989; Li, 2000). Most of the groups surrounding the park, including the indigenous *To Lindu* of the Lindu valley, were converted to Christianity when it was introduced by the Salvation Army during the Dutch conquest. Although at this time the *To Lindu* population subsisted primarily on *ladang*[2] agriculture, consisting of maize, tubers and other dry crops, they also practiced wet-rice agriculture, as evidenced by the remains of previously worked wet-rice fields found by the Dutch (Acciaioli, 1989).

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[2] Shifting cultivation

The Lindu valley remained a relatively isolated enclave throughout the colonial era and post-independence, primarily due to official government policy of discouraging immigration to the enclave by restricting education and health care facilities (Schweithelm et al., 1992). Nonetheless, this area has witnessed the arrival of other Kaili from Kulawi, as well as Bugis people from South Sulawesi, who are attracted to the area for wet-rice agriculture, perceived available land for the planting of important cash crops, like coffee and cacao, and the development of a fishing industry at the 3,000 ha lake. Although wet-rice agriculture (*sawah*) predominates in Lindu, and is practiced by both indigenous Lindu and migrants, tree cash crops, such as coffee and cacao, have become an important part of the Lindu economy.

An increase in human population size due to in-migration has resulted in a shortage of available land in many areas of the park, including the Lindu valley (CSIADCP, 1997; Bynum et al., 1999). Major pressures on the park include increasing human settlement in less than desirable areas, such as steeper slopes, with inevitable consequences in the form of landslides and erosion, the occupation of lands within the park's boundaries, and unauthorized harvesting of resources within the park (CSIADCP, 1997).

METHODS

Data collection and analysis

I collected information on perceptions of the forest, the National Park, and conservation through informal and formal interviews with villagers from Anca and Tomado from June 2002 to April 2004. Respondents for the formal interviews were selected using a chain-referral approach (Bernard, 1995). Interviews were conducted with both indigenous *To Lindu* and migrants to ensure adequate sampling of the potential variability in perceptions held by people of different ethnicities and backgrounds. All interviews were conducted in Bahasa Indonesia by the author and then translated into English. For the formal interviews, I asked respondents the following questions: (1) what is the purpose/function of Lore Lindu National Park, (2) what are the benefits of the National Park, (3) what are the negative outcomes of the National Park, (4) what are the threats towards the National Park, and, (5) what are the benefits of conservation. Although these questions were treated as freelists on a particular domain of knowledge (e.g., purpose of a National Park), respondents elaborated on their responses as they felt necessary. I then coded these open-ended responses into practical categories (Fleisher & Harrington, 1998). For example, the response, “protect everything in the forest so that it does not go extinct,” to the first freelist question was coded as “nature protection.” Responses such as “protect wood, rivers, forest resources, wildlife and plants,” however, were coded as “protect resources.” These freelist data were then analyzed using ANTHROPAC 4.983 (Borgatti, 2004) to determine which categories were the most salient. Salience is a measure of how much knowledge respondents have and how important that knowledge is to them (Fleisher & Harrington, 1998).

I then used consensus analysis (Romney et al., 1986) to further explore whether respondents share common perceptions regarding the National Park and its conservation. The basic assumption behind consensus analysis is that agreement among respondents indicates shared knowledge. Consensus analysis conducts a minimum residuals factor analysis of the similarities among the respondents, adjusted for random variation (Handwerker, 1998). A ratio of at least 3 to 1 between the eigenvalues for the first and second factors in the solution is generally accepted as evidence of shared beliefs. The degree to which a respondent agrees with the consensus—the respondent’s *cultural competence*—is represented by his/her score on the first factor (i.e., the pattern that explains the maximum amount of variability among respondents). These scores typically range from 0 to 1, with higher scores (e.g., 0.8), indicating that the respondent agrees with the consensus (Curry et al., 2002).

In consensus analysis, the number of respondents needed to produce valid results increases as the overall level of agreement among respondents decreases (Romney et al., 1986). If the level of agreement for a group is suspected to be low, researchers who use this technique typically select a sample of 25 – 40 respondents to ensure that valid results can be obtained (Weller et al., 1999). I conducted interviews with 45 respondents. The age of respondents ranged between 31 – 73, with the average age of 53. The majority of the respondents were male (71%). Forty-nine percent of the respondents were indigenous *To Lindu* while the other half were migrants from other areas of Central Sulawesi (15 respondents), South Sulawesi (7 individuals), and North Sulawesi (1 respondent).

Informal discussions with villagers upon my arrival in Lindu revealed that *To Lindu* folk ecology includes stories about human-macaque interactions. Respondents for the formal interviews were therefore asked to recount folklore they knew regarding the relationship between humans and macaques, human-macaque interactions, or human-macaque conflict. In order to fully document this folklore, I also conducted informal interviews with individuals who were identified by other villagers as ones who knew the stories. These interviews were tape recorded with permission and subsequently transcribed by a field assistant. I then translated the transcribed interviews from Bahasa Indonesia to English.

RESULTS

Perceptions of the National Park and conservation

Nature protection[3] was the most salient category of the purpose of the National Park for the respondents (Table 5.1). There was no consensus, however, among them on what categories should be included in this domain (ratio = 2.11). When the data were analyzed by ethnicity (i.e., two groups: Lindu and migrants), the results indicated that among the Lindu "nature protection" had the highest salience score (0.77), and there was agreement among them on the purpose of the National Park (ratio = 3.47; mean level of agreement = 0.72, SD = 0.33). Among migrants, however, "nature protection" and "don't know" had the two highest saliency scores (0.57 and 0.39, respectively), and there was no consensus among them on what categories should be included in this domain (ratio = 1.3).

Table 5.1. Results of freelist analysis and consensus analysis overall and by group

Freelist questions and responses (categories)	Overall Salience[a]	Salience (Lindu)	Salience (Migrants)	Consensus?
Purpose of LLNP				
Nature protection	0.667	0.773	0.565	Overall: N
Don't know	0.267	0.136	0.391	Lindu: Y
Protect resources	0.089	0.159	0.043	Migrants: N
Prevent erosion, flooding etc.	0.033	0.023	0.022	
Tourism	0.022	0.045	-	
Benefits from LLNP				
Resources	0.411	0.5	0.326	Overall: N
Prevent erosion, flooding etc.	0.233	0.295	0.174	Lindu: N
Nature protection	0.211	0.227	0.196	Migrants: N
Don't know	0.178	0.091	0.261	
None	0.044	0.045	0.043	

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[3] Responses coded as "nature protection" included mention of extinction prevention (e.g., "protect everything in the forest so that it does not go extinct") and preservation for future generations (e.g., "so our grandchildren can see it [nature] in real life").

Tourism	0.022	-	0.043	
Negatives of LLNP				
None	0.422	0.545	0.304	Overall: Y
Restricted agricultural development	0.244	0.045	0.435	Lindu: Y
Don’t know	0.133	0.136	0.130	Migrants: N
Restricted forest product collection	0.067	0.045	0.087	
Limited economic development	0.100	0.114	0.087	
Migrants	0.067	0.136	-	
Crop raiding	0.022	-	0.043	
Threats to LLNP				
Rattan collection	0.294	0.25	0.337	Overall: Y
Timber collection	0.106	0.049	0.159	Lindu: Y
Erosion, flooding etc.	0.189	0.136	0.239	Migrants: N
None	0.2	0.136	0.261	
Migrants	0.156	0.227	0.087	
Hunting	0.078	0.087	0.069	
Don’t know	0.111	0.091	0.13	
Agricultural expansion	0.056	0.114	-	
Road construction	0.044	0.091	-	
PLTA dam	0.022	0.045	-	
Lack of park guards	0.022	0.045	-	
Population size	0.011	0.023	-	
Benefits of conservation				
Nature protection	0.444	0.5	0.391	Overall: N
Prevent erosion, flooding	0.256	0.182	0.326	Lindu: N
Resources	0.233	0.25	0.217	Migrants: N
Don’t know	0.156	0.136	0.174	

[a] Salience scores take into account the number of freelists in which the category appears, and the average position in which the category appears in freelists.

The most salient benefit of the National Park for the respondents was “resources” (Table 5.1). Forest resources listed by respondents included rattan, wood, wildlife, and water. Respondents did not show consensus, however, on what categories should be included as benefits of the National Park (ratio = 2.5). Although both the Lindu and migrants listed “resources” as the most salient benefit, the second most salient benefit differed between the two groups: the Lindu listed "prevention of erosion, flooding, and landslides" while migrants listed "don't know." There was no consensus among the Lindu (ratio = 1.95) nor among migrants (ratio = 2.26) on the benefits of the National Park.

The most salient negative outcome of the establishment of the National Park for all respondents was that there were none, and there was consensus among them (ratio = 3.23; mean level of agreement = 0.72, SD = 0.21). Analysis by ethnicity revealed that "none" was the most salient negative outcome (Salience = 0.55) for the Lindu, while "limited agricultural development" was the most salient negative outcome (Salience = 0.44) for migrants. There was consensus among the Lindu (ratio = 4.39; mean level of agreement = 0.71, SD = 0.31), while among migrants there was no consensus (ratio = 1.82). This disparity between the Lindu and migrants was also evident by statements made by some Lindu and migrants (e.g., Bugis from South Sulawesi) on how each group lives their lives:

> The more we have, they happier we are, and the more we still want. As for the Lindu…..they figure all is well the way it is…if they have a house that is good enough, there is no need for a better one…..but really they are just jealous of us. (Bugis resident of Tomado)
>
> After having been given land, they [Bugis] want more. (*To Lindu* villager)
>
> They [migrants] go into the forest and make more gardens. (*To Lindu* villager)
>
> Lindu people like looking at the forest….and rattan that we need isn't too far away here. (*To Lindu* villager)

The most salient threat to the National Park, overall as well as within each group, was rattan collection (Table 5.1). In addition, there was consensus among the respondents on what categories should be included as threats to the park (ratio = 4.54; mean level of agreement = 0.75, SD = 0.13). The two groups differed, however, on what they considered the second most salient threat; the Lindu listed migrants, while the migrants themselves listed "none." That the Lindu envision migrants as threats stems from their fears of the over-exploitation of forest resources and the disregard of Lindu *adat*[4] by migrants: "transmigrants don't know the rules of Lindu *adat* about the forest….they only feel that they can benefit from it" (Lindu male, 30s); "the Bugis want more land even after they have been given some" (Lindu male, 70s).

Freelists of the benefits of conservation indicated that the most salient responses were nature protection; prevention of floods, erosion, and landslides; and the protection of forest resources, with no apparent consensus on these benefits (ratio = 1.41). When analyzed by ethnicity, nature protection was the most salient category for both the Lindu (Salience = 0.5) and migrants (Salience = 0.39), but there was no consensus within each group on what categories should be included as benefits of conservation (Lindu: ratio = 1.99; Migrants: ratio = 1.56).

<u>Human-macaque folklore</u>

A total of 24 respondents from the formal interviews were asked if they knew of a story or stories regarding the relationship between humans and monkeys. Of these respondents, 58% (n =14) knew a story. Nine of them were Lindu, and four were migrants. Three interrelated themes emerged from the responses regarding human-macaque interconnections. The first theme was characterized by explanations of the origin of monkeys, and by statements that pointed to human-monkey similarities. These statements, from both Lindu and migrants, included:

> A human was burned within grasses and became a monkey. This is just talk, though, not a belief, because there is no way monkeys are from humans. (Lindu male, 70s)
>
> They are from the *esa*[5]. While burning the garden….a monkey with a red butt left…. (Lindu female, 50s)
>
> There were two women who loved one man. These two women fought in the forest and one of them burned and became a monkey. (Lindu male, 70s)
>
> Two women were collecting *esa*, a man burned the area with the women, and became a monkey. (Lindu male, 60s)

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[4] *Adat* is typically defined as the customary laws (e.g., local traditions and natural resource management practices) developed by the members of various sub-ethnic groups. Increasingly, it is being viewed as a dynamic institution which is continually being reinvented (Tsing, 1993; Peluso, 1995).

[5] *Esa* is the Lindu word for a type of grass.

> The story from *orang tua*[6] is the people gardening wanted to burn the area but they couldn't get out, so they burned and became monkeys. (Lindu female, 30s)
>
> Monkeys and people are on one line—whereby a human fell into a cooking pot and burned…it lost its butt and its hair turned black. I think it makes sense, we have the same hands. (Migrant male, 40s)
>
> Monkeys are from people, because they have five fingers too. A human was thrown from the house to the forest and there it became a monkey. (Migrant female, 40s)
>
> Monkeys are regarded as kin [by the Lindu]. It is reciprocal relationship…monkeys will shake a mango tree such that the fruits fall so that we don't have to climb the tree. (Migrant male, 50s)

The second theme, concerning human-monkey interactions, stems from a story told only by the Lindu, and specifically those from the village of Anca, on a specific human-macaque interaction that now shapes their attitudes towards Tonkean macaques. Informal interviews with three elders from the village of Anca revealed the specifics of the story. Below is the full story as told by a Lindu male elder (age = 69) from the village of Anca:

> This story dates back before the arrival of the Dutch. I heard this story when I was still in school because at that time when I came home from school I had to go and guard the gardens.
>
> A man lived with his teenage daughter. One day, this man instructed his child to stay at the house because he had to go check his fish nets. He told his child that if the monkeys came, to talk harshly with them and say that they are not allowed to come here and disturb our crops. What's more is that there were many chicken eggs in the house. At 8:00 or 8:30 in the morning hundreds of monkeys came; they ate maize and squash. The garden was all black because it was full of monkeys. Next, the monkeys began approaching. The young girl began telling them just like what her father instructed her to do: "you monkeys are not allowed to bother us or to eat our crops," but the monkeys continued to approach her until they reached the house. They entered the house, and the young girl began beating them with coals from the fire but the monkeys would not leave, and then ate all of the chicken eggs. After all the eggs were gone, they caught the young girl and left the house for the mountains. There was no one in the village because everyone was at the island Bola for a big *adat* party for three villages. At this time swidden agriculture was still practiced. The monkeys screamed and made lots of noise because they were happy that they had caught the little girl, and then they went to the forest. The hair of the young girl kept getting caught in thorns, but the monkeys just kept tugging on her. Her clothes were also caught in thorns and so were covered with holes. The entire time the little girl never fell to the ground because there were so many monkeys. Half of them cried out like humans. They then crossed over seven mountains.

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[6] *Orang tua* (Bahasa Indonesia) is typically translated as "parents," but in these narratives it means "ancestors."

> Meanwhile, the father heard all the noise and commotion from the lake, so he quickly paddled his way back and went home. He left all the fish, maybe more than 100 that he had caught in the canoe. He went straight to the garden and saw that his child was no longer there. He grabbed his machete and chased after them over 6 mountains. As he climbed he couldn't hear them but this was because they were already at the bottom of the 7th mountain. So he descended as well. He climbed a tree and saw his child sitting on top of a flat rock surrounded by seven rows of monkeys. The child was wrapped in traditional *mbesa*[7] cloth that belonged to the monkeys. He then began to approach the child while the monkeys were singing because they were happy because they got a human gift (the child). From about 4 m from where the child was sitting, the father leaped and grabbed his child, using the *mbesa* cloth to carry her. He then pulled out his machete and the monkeys began climbing his body until his skin was torn. But he didn't care because the monkeys were trying to get the child back. He then began using his machete to kill the monkeys until there were two left; one male and one pregnant female, and then the father took his child away. He continued to hold onto the machete with all the monkey blood on his hand. From the mountain he bypassed the hut and took the child straight to the island. At the island, he held a welcome home celebration for his child by slaughtering a water buffalo. So that's it…you can't just talk badly to monkeys because according to the story, monkeys are people too.
>
> Monkeys eat cacao because they are mad because people cut down their fruit trees so there is less monkey food.
>
> Others don't want to get angry with the monkeys because they know this story…if we are angry then the monkeys will do something like what happened with the father and his child. Therefore we can't leave behind teenage children or the monkeys will take them.
>
> This story has always been here, and will continue to.

None of the respondents from the formal interviews could recall this story. They did, however, talk about human-macaque interactions by making statements concerning how villagers should respond to monkeys that they encounter in the forest or in their gardens. These sentiments appear to be derived from the story told above. For example:

> Don't bother them because they will become even madder [than you]….just speak nicely to them. (Lindu male, 50s)
>
> Don't speak badly to them because then they will be mad. People give them a bit of corn on the outside of the fence and say, "here this is for you," until they don't eat our harvest anymore. (Lindu male, 70s)
>
> I've tried giving them a portion [of the harvest], instead of trying anything else, because they will be more mad if you do….like if you shoot at them. (Migrant female, 40s)

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[7] *Mbesa* is highly valued cloth that was originally traded by the Toraja with the *To Lindu* for water buffalo.

> You must respect monkeys even if they enter the maize and squash gardens—you give them a portion. (Lindu male, 60s)
>
> If you do something bad to them, they will come and disturb us. You leave a few fruits for them, and that is all they will take. (Migrant male, 60s)
>
> If monkeys come to our gardens we can only shoo them away…you can't be harsh because otherwise they will get angry. (Lindu male, 40s)
>
> If you talk bad to them [monkeys], you will become their enemy. (Lindu male, 40s)

The third theme, which only emerged from narratives from the Lindu, pointed to the belief that monkeys act as guardians of Lindu *adat*:

> Monkeys would give a sign if there was a *masalah hamil*[8], by destroying the garden, and killing dogs and water buffalo. So, we must take one animal, take its blood, take it to the water and deposit it there, so that everything will be all right…. (Lindu male, 50s)
>
> Monkeys took a buffalo from Anca. *Adat* was not followed so they took a water buffalo. (Lindu male, 60s)
>
> In the past our ancestors made a mistake. A disrespectful courting resulted in a pregnancy, so the buffalo of people here was caught and attacked by all the monkeys of Anca until the buffalo was dead. According to our ancestors' understanding of it, the spirits in the forest were embarrassed because the illegitimate pregnancy was not talked about well but instead the reality was that it was kept quiet. The buffalo was killed by the monkeys as a sign that something bad was committed and that the spirits were angry about it, the land was made filthy....this is the story from our ancestors, and almost everybody knows it. The monkeys are really cruel here…if there has been a problem they will alert us....gardens will be destroyed.
>
> People think that if gardens are destroyed, then it is obvious why. But gardens are destroyed by all animals. It is like the maize gardens up the mountain.....we know that the monkeys destroy the garden…but if the garden is in a place like that there is no problem because it is close to the forest but if it happens in the village, then people start looking for the reason. If it is found, then *adat* must be quickly carried out, and then it will be safe again.
>
> If monkeys come to the gardens one must not speak harshly to them, or throw anything at them…or be mad at them, for then they (monkeys) will retaliate. Usually one says, just take it [crops] or just eat it, but leave us some too, and once you have your share, go on home. (Lindu female, 70s)

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[8] A literal translation from Bahasa Indonesia would be "problem pregnancy." In this context, it means "illegitimate pregnancy."

When asked whether she still thinks people believe the story, she responded:

> Yes, there are one or two. It is not that evident anymore. Although people here go to church, they still don't want to do anything harsh to the monkeys. If we think of them as creatures of God's power as well, if they come to bother us we just tell them to leave….but don't kill them. People here are still scared…when doing stuff don't let it result in like what was experienced by those in the past…don't be brave and try …whatever our ancestors said is right because they have already experienced it; that is, if a monkey is killed, perform *adat* in which a buffalo is offered and slaughtered, so that the sick ones could become healthy again. So we have already found religion…but don't dare to kill an animal like the monkey. If you find them in the garden tell them to leave. We are vigilant when it comes to the monkeys, we don't just kill them for there will be an effect. If you follow the story that monkeys descended from humans then this means that we are kin.

DISCUSSION

Primate conservation research that focuses on the ecological indicators of survivability and the documentation of major threats to nonhuman primates is important because it contributes to the development of conservation action. An important area that is typically neglected in such work, however, is attention to culture; that is, environmental ideologies and behavior of the people living in and adjacent to nonhuman primate habitats. Human societies have elaborate cultural beliefs, values, and customs regarding forests and wildlife, including nonhuman primates (Sponsel et al., 2002). Research that investigates not only what people do in relation to their environment but *why* people do it may better inform conservation efforts. This was the intention of the research reported here. By examining villagers' conceptualizations of Lore Lindu National Park, its conservation, and the nonhuman primates within, I provide a more nuanced and complete picture of the context in which conservation initiatives in Lore Lindu National Park should take place.

Multiplicity of the "local" and environmental values

Boonzaier (1996) acknowledges that attitudes are often difficult to assess because they represent complex and nuanced beliefs, and because members within the local community may not all share the same attitude toward conservation. For example, in areas of high in-migration, such as Lore Lindu National Park, a resulting diversity in backgrounds (i.e., ethnicities, lifestyles) may translate into differing views, concerns, and interests with regard to forest use and protection (Ostrom, 1999). The results from the research indicate that within the community of Tomado, there is considerable diversity in local knowledge, attitudes, and perceptions of the forest and its conservation that vary by cultural-ecological and ethnic identity. Among the indigenous *To Lindu*, there was strong agreement on the purpose of the National Park, with nature protection being the most salient response given. In contrast, there was no consensus among migrants, many of whom did not know the purpose. Similarly, the second most salient response listed by migrants as a benefit of the National Park was that they don't know. These results may reflect the fact that many of the migrants (e.g., Bugis) have limited knowledge of and interaction with the forests of Lindu. These findings suggest that knowledge about protected area conservation may be linked to place (Basso, 1995; Hunn, 1999; Atran et al., 2002; Casagrande, 2002). The statement from a Lindu villager of Anca, "local wisdom is the reason we guard the wildlife of the forest," confirms such a link; the lives of indigenous *To Lindu* are more intricately intertwined with the local ecology, thus resulting in greater environmental knowledge, awareness, and action.

Perceptions of the impact of the establishment of the National Park on villagers' livelihoods also varied between the indigenous *To Lindu* and migrants; the most salient category for the Lindu was that there were no negative outcomes, while limited agricultural development was the most salient for migrants. These divergent views suggest that there are fundamental differences between the Lindu and migrants in the ways the forest is conceptualized; the Lindu conceptualize the forest as a source of livelihood (e.g., resources) and speak to the value of its persistence for future generations, while migrants envision the forest as an area that should be cleared for additional agricultural development (i.e., rather than a space to be preserved). These results point to the existence of significant intra-local variation in perceptions of the environment that guide action in that environment (Nazarea et al., 1998; Atran, 1999).

Although local perceptions of the forest and its benefits tend to differ from those held by conservation organizations (Casagrande, 2004), this does not mean that that local people do not perceive non-utilitarian values of protected areas (Newmark et al., 1993; McLean & Stræde, 2003). In this study, the finding that there was no consensus among respondents on the benefits of the National Park suggests that there is considerable variation, both intragroup and intergroup, in villagers' perceptions of the benefits of a protected area and conservation. Categories listed by respondents included viewing the National Park as a place for acquiring forest products (e.g., rattan, wood, water, etc.), as a source of important services (e.g., watershed protection, which impacts their livelihoods as agriculturalists), and as a source of intrinsic value (e.g., to ensure future generations can also appreciate the forests and wildlife). These results suggest that the way people conceptualize "value" do not necessarily represent only one type or another (i.e., utilitarian or intrinsic). In Lindu, values people imbue the National Park are parallel to what Ellen (1993: 139) found among the Nuaulu: they are "multi-faceted and differential, simultaneously materially useful and culturally meaningful."

Folklore: culture for conservation?

The three themes that emerged from respondents' narratives of human-macaque interactions demonstrate that villagers in the Lindu valley possess folklore that that envisions monkeys and humans as interrelated biologically, ecologically, and culturally. Both the Lindu and migrants speak to the biological and morphological similarities between macaques and humans, and some even refer to the macaques as kin. It is among the indigenous *To Lindu*, however, that the cultural linkages between macaques and humans are most salient; the macaques are linked to the Lindu via *adat*. Moreover, although two of the respondents that spoke to how humans should behave in relation to monkeys were migrants[9], the detailed human-monkey kidnapping story was told only by the Lindu. This story, however, was only recounted in its entirety by elders in the village of Anca; no person under the age of 50 could recall the story. This finding illustrates an important feature of people's attitudes and beliefs; they are not cultural fixed points, eternal and unchanging (Knight, 1999; Hill, 2002). The use of cultural arguments for primate conservation is seen as problematic for this very reason. For example, among the Iban in Kalimantan, Indonesia, Wadley et al. (1997) found that conversion to Christianity has resulted in many people abandoning previous taboos against the killing and eating of orangutans. The Lindu valley has witnessed a similar pattern. In the past, the felling of fig trees was taboo because evil spirits were believed to reside within the trees (Riley, in prep c). This taboo has had a conservation outcome because it resulted in the protection of strangling forms of the genus *Ficus*, species that are important Tonkean macaque foods (Riley, in prep. a), and that are considered the single most important food source for Sulawesi's fruit-eating birds and mammals (Kinnaird et al., 1999). Today, many villagers indicate that the predominance of religion (i.e., Christianity) now negates the belief in evil spirits. A changing sociocultural environment has therefore resulted in the relaxing of a cultural taboo that may ultimately negatively affect the survivability of wildlife that depend on fig fruits.

Human-macaque folklore in Lindu, however, appears to not necessarily have been affected by the conversion of the *To Lindu* to Christianity. Instead, the inability of younger

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[9] These two individuals originated from Kulawi, and thus are members of another Kaili group. Their statements may therefore reflect similar folklore held among the Kaili of Kulawi.

residents to tell the story may reflect limited transmission of knowledge across generations, as well as changing ecological and socioeconomic conditions in Lindu (i.e., shift from traditional *ladang* agriculture to wet-rice agriculture, cash crops, and fishing as the major sources of livelihood) (e.g., Ross, 2002). Nonetheless, what does remain salient among younger Lindu residents is not so much the details of the story, but rather its essence (i.e., "If you talk bad to them [monkeys], you will become their enemy"); a belief that continues to guide people's behavior as they relate to monkeys, even if they are unaware of the origin of the belief. This suggests that among the younger Lindu generations there remains a sense of strict adherence to tradition (i.e., "that is what our ancestors told us"), regardless of its meaning or origin. This story likely explains why the *To Lindu* tolerated crop raiding by macaques in the past and continue to tolerate it, and although only remnants of the story remain, these remnants of human-macaque folklore may help to ensure the persistence of macaques.

On the other hand, migrants who do not possess such folklore and whose cacao gardens are also raided by macaques, may have no qualms about defending their crops—their source of livelihood—by any means necessary (e.g., Salafsky, 1993). The ability of macaques and humans to coexist at the forest-agriculture ecotone may therefore ultimately require that farmers perceive a utilitarian basis to macaque preservation (Knight, 1999). For conservationists, this might mean working towards a convergence of values (Harcourt et al., 1986; Weber, 1987). Species preservation, typically a strictly intrinsic value approach, may have little significance for migrant villagers in Lindu who do not possess folklore regarding the cultural and ecological relationships between humans and macaques, and who experience crop loss due to raiding macaques (Riley, in prep. c). It is also possible that human-macaque folklore held by the *To Lindu* may eventually be abandoned with changing sociocultural and economic realities. For example, there are some in Lindu who know the story but who have chosen to disregard it:

> He has already heard the story but he is not afraid…but maybe later there will be a problem. He really doesn't want to do it [make traps] again, after I talked with him. [he] said: "as opposed to father tiring out having to go there every day, I want to kill them all. I put traps up along the entire maize crop so that each time they enter they will be finished. I said "don't you do that." After I spoke that way he didn't want to do it again. (Lindu female, 70s, talking about her son's frustration with crop raiding macaques)

A species preservation value may be more meaningful to villagers if they recognize the important roles nonhuman primates play in forest ecosystem dynamics. The ecological impact of nonhuman primates on forest community dynamics through their role as major seed dispersers has been a primary focus for many recent primate ecological studies (Chapman, 1996; Chapman & Onderdonk, 1998; Lambert & Garber, 1998). Documentation of primate seed dispersal of tree species that have economic and/or cultural value for villagers, such as the work conducted by Lambert (1998) in Kibale National Park in Uganda, may provide a strong argument for the protection of nonhuman primate populations, one that bridges both western conservation values and local values. In Lindu, if Tonkean macaques are major seed dispersers for forest resources that are highly valued by villagers (e.g., *Elmerillia ovalis, E. tsiampaccca,* and *Arenga pinnata*: Riley, in prep. c), by both indigenous Lindu and migrants alike, the preservation of macaques may become important for the community as a whole.

Conclusions

"True conservation" has been defined by Smith & Wishnie (2000:501) as "actions or practices that (a) prevent or mitigate resource depletion, species extirpation, or habitat degradation, and (b) [are] designed to do so." Although the findings from Lindu do not necessarily fit this definition, the persistence of human-macaque folklore and the behavioral patterns that result from it may ultimately have a conservation outcome if taboos against harming the macaques continue to protect them in areas of human-macaque overlap. Furthermore, the fact that villagers perceive threats to the National Park and show consensus in their beliefs may also allow for greater environmental awareness and action within the community (Kottak & Costa, 1993). Conservation efforts in Lore Lindu National Park that incorporate a two-way system of education and involve local people in conservation and research may be successful in reinforcing these positive customs and perceptions of forest and wildlife that do favor conservation (Kuriyan, 2002). It may also be more appropriate for conservation initiatives in the park to concentrate on environmental problems that are a real concern to the community, as determined from this study's ethnography (e.g., prevention of floods, erosion, and landslides, and the protection of forest resources), which may act as more powerful incentives against forest degradation for all community members than the Western value of species preservation.

This research also illustrates the need to carefully consider *who* it is that we mean by "local" and to understand, address, and attempt to integrate the varying local viewpoints when enacting conservation efforts. For example, the finding that there is considerable diversity in environmental conceptualizations in Lindu that varies by cultural-ecological and ethnic identity can better inform the implementation of collaborative community conservation such as the efforts initiated in Lore Lindu National Park. In at least 40 villages around the park, attempts at a decentralized system of natural resource management have included the development of negotiated agreements of collaborative natural resource management between local communities and state agencies, in cooperation with several nongovernmental organizations (NGOs). These negotiated community agreements, *Kespakatan Konservasi Masyarakat* (KKM), work in conjunction with the official village government (*kepala desa*) and the traditional village council (*Lembaga Adat*) to create a new local institution, *Lembaga Konservasi Desa* (LKD), that will oversee the implementation of the KKM and the community's commitment to it. The meeting held in Tomado on Nov. 15, 2003 to initiate the LKD, however, included members of the traditional village council and village government, all of whom except for one were indigenous Lindu people. Given the diversity within the community in conceptualizations of the environment, it may be insufficient and unproductive to only enlist village members whose views may only represent a portion of the community. To establish an effective local institution, diverging perceptions and concerns within a community must be explicitly addressed. The collaborating NGOs may then be able to play a critical role in facilitating a convergence of interests within the community.

Although there has been a recent call among some members of the conservation community for a renewed emphasis on strict protection through authoritarian enforcement practices (e.g., Oates 1999; Terborgh 1999), there remain many who believe that the success of international biodiversity conservation rests on our ability to maintain open dialogue and work towards concerted negotiation (Brechin et al., 2002). This approach requires that we recognize that there are different ways of understanding and appreciating the natural world, and that we must pay attention to historical factors, as well as broader social and political factors that shape people's attitudes towards nature, protected areas, and conservation (Peluso, 1996; Wilshusen et al., 2002). There is unlikely to be one single solution or principle to be used in primate conservation, as different circumstances call for different combinations (Strum 1986). A recent surge of interest in ethnoprimatology points to a growing awareness that the way in which we conceptualize the environment translates into the way we approach its conservation. By focusing on an interaction paradigm (i.e., humans and nonhuman primates as members of a dynamic ecosystem) rather than a pristine paradigm, ethnoprimatology encompasses a flexible approach to the integration of the interests and concerns of both human and nonhuman primates (Fuentes & Wolfe, 2002).

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CHAPTER 6

CONCLUSION

The four manuscripts in this dissertation together represent a multifaceted investigation of the interface of primate ecology, human ecology, and conservation in Lore Lindu National Park, Sulawesi, Indonesia. In this final chapter, I discuss the contributions of this research to primate ecology, the discipline of anthropology as a whole, and to the practice and process of conservation.

Primate ecology and conservation

Primate field studies, which began to proliferate within primatology in the 1960s, have fundamentally been concerned with the behavior and ecology of nonhuman primates in their *natural* environments. What this typically has meant is an examination of an ecological context that is free of human influence. It is likely, however, that living in close proximity with other primates has characterized much of our evolutionary history, during which humans and nonhuman primates competed, possibly directly and indirectly, for key resources in their shared environments for centuries, millennia, or possibly longer (Sponsel, 1997; Sponsel et al., 2002; Sprague, 2002). For example, based on cut-mark evidence on remains of *Paleopropithecus* bones from Taoloambiby, Madagascar, Godfrey & Jungers (2003) argue that it is possible that human hunting played a role in the extinction of at least some of the large-bodied subfossil lemur species. In Lopé, Gabon, it is believed that three genera of hominoid (*Pan*, *Gorilla*, and *Homo*) coexisted for a period of at least 60,000 years, whereby overlap existed in the plant foods favored by these genera, possibly resulting in competition among them (Tutin & Oslisly, 1995). The potential longevity of this sympatry then begs the question of whether one or more forms of human-nonhuman primate symbiosis (i.e., commensalism, predation, parasitism, competition, mutualism, etc.) necessarily represent an unnatural situation (Southwick et al., 1965). Furthermore, in the changing contemporary world, logging, development projects, and agricultural expansion increasingly result in the alteration and destruction of nonhuman primate habitat (Mittermeier & Cheney, 1987). The fact that all of these forces represent human activities challenges us to consider whether it is appropriate to continue to envision nonhuman primate habitats as pristine and undisturbed, free from human influence.

Primate community ecology has traditionally examined the ecological interactions among sympatric nonhuman primates in their natural environments. This dissertation contributes to this area of research by adding a new dimension to what is meant by “primate communities”: the “human-nonhuman primate community.” The idea of a “human-nonhuman primate community” moves beyond the notion of boundaries between humans and nature, and envisions human and nonhuman primates as members of a dynamic ecosystem. By doing so, our understanding of key concepts in community ecology, such as ecological niche and niche separation, are also expanded. Differential forest substrate use is one way that primate species alter their niche occupation (Reed & Bidner, 2004). As demonstrated in this dissertation, human habitat alteration results in a shift in niche occupation of Tonkean macaques; Tonkean macaques in human-modified habitats spend more time on the ground, and thus face potential conflict with humans who also occupy this niche in areas of overlap. More time on the ground means that Tonkean macaque foraging strategies may include foods that exist at this level, including both wild foods and anthropogenic foods (e.g., cacao). Crop raiding can therefore be viewed as an interesting example of niche competition rather than a side effect of abnormal ecological conditions (Richard et al., 1989).

Investigations of predation pressure on primate communities have also been central to a community ecology approach (e.g., Hart, 2000; Schultz et al., 2004). In the literature, however, human hunting is not typically discussed as a form of predation; "the extent to which human hunting can be considered along with nonhuman predation is questionable, as the former often causes much higher mortality rates in prey species than does the latter" (Reed & Bidner, 2004: 11). Given the potentially long history of human-nonhuman primate sympatry, which in some areas may have involved frequent human hunting of nonhuman primates (e.g., examples mentioned above), it seems critical that we incorporate humans as key actors in nonhuman primate predation (e.g., Peres, 1999).

This dissertation also contributes to our understanding of the ecological and behavioral flexibility of nonhuman primates in human-modified environments, as well as the conservation implications of such flexibility. The results indicate that Tonkean macaques can respond to anthropogenic habitat alteration by being flexible in their diet, by incorporating more alternative food items, such as insects, fungus, crustaceans, leaves and shoots of colonizing weeds, by exploiting resources that dominate human-altered areas (e.g., *Arenga pinnata*), and by adjusting their activity budgets to devote more time to foraging. Foraging can only be considered successful, however, if the diet obtained provides sufficient amounts of energy and other nutrients to fulfill nutritional requirements (Oftedal, 1991). A reliance on a small number of species for a majority of the diet for Tonkean macaques living in areas where disturbance is regular and increasing, as was observed in this research, may ultimately be a limited strategy if an inadequate array of nutrients is obtained, and if those key food species represent tree species highly valued and utilized by villagers for their livelihood needs. Figs are widely recognized as keystone resources for many tropical frugivorous vertebrates because their fruiting patterns result in a reliable food source during times of general fruit scarcity (Leighton & Leighton, 1983; Terborgh 1986). Figs may also serve as keystone food sources for Tonkean macaques, particularly for groups, like the Anca group, that live in disturbed habitats where fig species often thrive (Plumptre & Reynolds, 1994; Estrada et al., 1999; Fashing, 2001). In fact, fig fruits constituted the second largest proportion of the plant species diet for the Anca group. Leighton (1993) has shown, however, that fig pulp is nutritionally inferior to nonfig pulp and seeds (but see O'Brien et al., 1998). In areas of overlap with human forest use where other important macaque food trees (e.g., *Artocarpus* spp. and *Elmerilla* spp.) are felled, an increased reliance on fig fruits may mean that Tonkean macaques may be unable to obtain sufficient nutrients.

Tonkean macaques also appear to be flexible in how they move in space. For example, they can adjust their use of forest strata in order to facilitate travel and increase foraging opportunities (e.g., insects) on the ground. With regard to movement patterns, the abundance and distribution of the limited resources in heavily-altered environments may require significant movement on a daily basis, as was evident by the similar daily path lengths of the two groups, despite a substantive difference in group size. Because Tonkean macaques in the heavily-altered habitat intensively used particular areas within their home range, this research suggests that the key aspect of flexibility in movement may have less to do with the amount of area explored (daily and annually), but in how they *use* the area within their range (Ostro et al., 1999). Previous research has shown that range use is specifically related to the availability of key resources. For example, Olupot et al. (1997) found that intensity of quadrat use by gray-cheeked mangabeys (*Cercocebus albigena*) was significantly related to the number of fruiting trees/lianas in the quadrat. Agetsuma & Noma (1995) found that Japanese macaques (*Macaca fuscata yakui*) shifted their range to the areas where *Myrcica rubra* was densely distributed during fruiting seasons. Because there are fewer resources available in the Anca group's habitat, this group may have shifted its use of space to concentrate exclusively in areas where their preferred resources still remain, and where they can monitor changes in food availability more closely (Agetsuma & Noma, 1995). For example, this group would frequently return to the same tree to sleep during a 3-day sample period.

Although many researchers attempt to parcel out the effect of a particular variable on behavior (e.g., effect of group size on ranging patterns), others contend that primate behavior, such as foraging patterns and travel patterns, is best understood within the context of *multiple* interrelated factors including, for example, diet, morphological specializations, physiological constraints, as well as important ecological variables such as, habitat quality and the availability and distribution of food (Norconk & Kinzey, 1993). The results from the research presented in this dissertation lend support for the latter position. The small group size of the Anca group may be the direct result of diminishing habitat quality impacting mortality or producing fission in a once larger group. Fissioning represents one strategy, among others, that primate groups can employ when faced with changes in their environment that result in lower quality habitat (Dittus, 1988; Ménard et al., 1990; Lee, 1997). Groups will split and form new smaller groups that can forage in smaller food patches without depleting the patches (van Schaik et al., 1983; Johns, 1986; Rodman, 1988). The group size observed for the Anca group may be the optimal size in which foraging efficiency is maximized for the habitat (Stacey, 1986), and therefore may be the response, in conjunction with dietary and behavioral flexibility, to disturbance of their habitat.

The ability of nonhuman primates to be behaviorally and ecologically flexible to changes in their environments is facilitated by the existence of key food resources. Terborgh's (1986) observation of periods of general scarcity of fruit in a highly seasonal environment led to the concept of keystone resources: plant species that are predictably available during periods of food scarcity and that serve to sustain populations during these critical times. As noted above, figs are widely recognized as keystone resources for nonhuman primates as well as other tropical forest dwellers (Terborgh, 1986; Kinnaird et al., 1999; Fashing, 2001; Tweheyo & Lye, 2003; but see Gautier-Hion & Michaloud, 1989). This concept is not limited, however, to members of the genus *Ficus*; herbaceous vegetation (e.g., arrowhead and ginger) has been noted as keystone foods for gorillas and elephants in Gabon (White et al., 1995), and palms are recognized as keystone resources for some neotropical primates (Terborgh, 1983; Lehman, 2004). The palm *Arenga pinnata*, which produces fruits year round and thus offers a stable source of calories, may act as a keystone resource for Tonkean macaques that occupy human-modified habitats. Human-modified habitats, however, experience not only general periods of food scarcity due to seasonal changes in phenology, but *overall* periods of food scarcity due to the removal of important food trees. This contemporary reality, as it becomes more widespread, points to the need to broaden our understanding of the concept of keystone resources as functioning only during times of "natural" food scarcity, and instead, documenting key species that allow nonhuman primate to persist in their current states of *perennial* food scarcity. These data can then inform the conservation management tool of deliberately protecting particular wild food species known to be important for macaques, especially in areas where there is frequent overlapping resource use between human and nonhuman primates. For example, Naughton-Treves et al. (1998) recommended deliberate management of *Mimusups bagshawei*, an important fruit source for chimpanzees, as a means to alleviate crop raiding because they found that raiding of banana trees declined with increases in the availability of the fruit of this species. Bicca-Marques and Calegaro-Marques (1994) suggest that because the exotic orange tree (*Citrus sinensis*) is a staple food source for *Alouatta carya* living in marginal habitats, cultivation of this tree may allow black howlers to persist in those areas.

Ethnoprimatology: Bridging cultural and biological anthropology

The hallmark of the discipline of anthropology is its holistic approach to the question of what it means to be human. The accuracy of this hallmark is questionable, however, considering the fact that there has been a long history of division between cultural and biological approaches to the study of humanity (Paul, 1987a; Morell, 1993; Cartmill, 1994). Fortunately for the discipline, a number of anthropologists have attempted to identify of areas of convergence in hopes of reaching reconciliation. Paul (1987b) points out how there have been parallel developments in biological and cultural anthropology in emphasizing *individuals* as the strategizing agents. Some look to the link between primatology and human evolutionary ecology, with its attention to the evolution of culture and human behavioral ecology (e.g., Smith & Winterhalder, 1992) as a bridge between the biological and cultural realms of anthropological inquiry (Rodman, 1999). Matt Cartmill, in his annual luncheon address at the 1994 meeting of the American Association of Physical Anthropologists, admitted that biological anthropologists do have something to learn from more humanistic approaches; critical theory, for example, demonstrates how knowledge acquisition is often a political process rather than one of pure discovery[1]. Cartmill (1994) goes on to state that what is needed is not a retraction by biological anthropologists from their cultural colleagues, but rather an engagement between them. Yet still, in the new millennium, the question remains: can biological anthropology and cultural anthropology truly coexist as components of a "holistic" anthropology, given their traditionally disparate epistemologies and methodologies[2]. I would argue that ethnoprimatology, as exemplified in this dissertation research, has real potential to bridge these subfields. Ethnoprimatology's focus on ecological and cultural interconnections between human and nonhuman primates necessitates the use and integration of theory and techniques from both biological anthropology and cultural anthropology. It is for this reason that this new approach differs from previous attempts at reconciliation: rather than encouraging the adoption of biological methods to answer questions of culture, ethnoprimatology employs a multifaceted approach that embraces "multiple methodologies" (Orlove, 2003). Furthermore, because it also explores the conservation implications of ecological and cultural interconnections, it provides another avenue for anthropologists to contribute to effective and realistic conservation initiatives (Brosius & Russell, 2003).

Anthropology and conservation

Given the current realization that only a small amount of forested area actually falls within protected areas (i.e., 12 % of Earth's land surface: Chape et al., 2005), there has been a considerable amount of research exploring the conservation value of human-modified habitats, in particular agroforestry systems (e.g., Pimentel et al,. 1992; Estrada & Coates-Estrada, 1997; Greenberg, 1998; Moguel & Toledo, 1999; Donald, 2004). In Lore Lindu National Park, however, where cacao gardens are subject to raiding not only by macaques but also by two other

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[1] A good example is Celia Lowe's work (2004) in which she contends that the transformation of the Togean macaque from "new form" to "endemic species" was a strategic means to legitimize a Togean conservation project that would attract significant international funding.

[2] A plenary session at the 2003 meetings of American Association of Physical Anthropologists meeting, entitled "Can Biological and Cultural Anthropology Coexist?," addressed this concern.

mammal species, the recommendation of encouraging shade cacao as a buffer zone crop adjacent to forest reserves (Greenberg, 1998) may not be a suitable management tool. The results from this dissertation research do point to an alternative management strategy of discouraging additional planting of cacao in areas close to the forest edge and far (>500m) from the village, and encouraging more shade coffee in lieu of cacao at the forest boundary. Shade coffee has been proposed to be one of the most desirable land uses for buffer zones around protected areas (Petit & Petit, 2003), not only for bird populations but for primate populations as well. For example, McCann et al. (2003) found that howler monkeys in Mombacho, Costa Rica rely on trees in areas of active shade coffee cultivation for food, travel, and rest, suggesting that shade coffee plantations serve as a vital refuge for howlers in Mombacho. Furthermore, appeal to the ever-growing market for products with low environmental impact (i.e., “green markets”) can provide an incentive for farmers to enhance and protect traditional coffee production methods (Greenberg, 1998; Albertin & Nair, 2004). In Lindu, coffee is the second most important crop for villagers, both indigenous *To Lindu* and migrants, next to wet-rice agriculture (*sawah*). The animals that raid cacao gardens as determined by this research (i.e., macaques, squirrels, and forest squirrels) do not raid coffee plants, making this tree crop potentially more productive than cacao for farmers in Lindu, despite the price differential.

In places like Lindu, another suitable management strategy may be to explore ways to increase local tolerance to human-macaque conflict. One approach would be to examine the role of macaques in the regeneration of forest species that have economic and cultural significance for villagers. For example, Lambert (1998) found that a large percentage of plant species that have economic and/or cultural value to local Ugandan inhabitants at Kibale National Park are dispersed by a number of the frugivorous primates in the park. This finding suggests that maintaining populations of primates is important not only for forest regeneration, but also for human habitat use, and thus provides a strong argument for the protection of nonhuman primate populations. Important future research could address whether Tonkean macaques act as major dispersal agents for plant species in Lore Lindu National Park, and whether these species are important forest resources for humans. These data would then contribute to the promotion of a species preservation value approach to conservation that is more meaningful to villagers living in and around the park.

The future of conservation in Lore Lindu National Park and other protected areas, however, must be considered in light of the current sociopolitical context of resource management in Indonesia. The post-New Order period in Indonesia has brought dramatic changes to many aspects of governance, particularly in the realms of decision-making processes and natural resource management (Thorburn, 2002). In 1999, a year following the fall of president Soeharto, laws were passed that fundamentally altered the relationship between Jakarta and the regional governments, conferring administrative and regulatory authority to provincial and district governments (Barr & Resosudarmo, 2001; Thorburn, 2002; Djogo & Syaf, 2004). The implementation of decentralization in Indonesia, however, has faced a number of challenges. For example, the decentralization to local governments of the authority to manage forest resource has resulted in situations where those now responsible are accountable neither upward to the central government nor downward to the local people (Djogo & Syaf, 2004). In Jambi, Sumatra, for example, there has been no clear coordination among organizations mandated to represent the central government at the provincial and district levels. National Parks are under the control of the National Park agency, which reports to the Ministry of Forestry in Jakarta, and not the district government. As a result, the district government is ignorant of their responsibilities to protect conservation areas and to bear the costs of conservation (Djogo & Syaf, 2004). This problem is further exacerbated by corruption, whereby loggers are often protected by the military and police and by officials of district forestry services (Djogo & Syaf, 2004). On the positive side, decentralized systems of forest management can result in improved understandings of the specific biophysical, social, and institutional conditions influencing forest management at the level of the field, and greater access to local knowledge about the utilization and management of forest resources, which may lead to more sustainable and equitable use of those resources (Carney, 1995).

In Lore Lindu National Park, attempts at making a decentralized system work have included the development of negotiated agreements of collaborative natural resource management between local communities and state agencies, in cooperation with several nongovernmental organizations (NGOs). These negotiated community agreements, *Kespakatan Konservasi Masyarakat* (KKM), initiated in at least 40 villages at the park, work in conjunction with the official village government (*kepala desa*) and the traditional village council (*Lembaga Adat*) to create a new local institution, *Lembaga Konservasi Desa*, that will oversee the implementation of the KKM and the community's commitment to it, and initiate participatory conservation efforts within the community. What is considered particularly important about these local institutions is that they will have the authority to employ *adat* to decide upon sanctions to impose on those who violate the regulations of the agreement (Mappatoba & Birner, 2002). Although these agreements are ideal because their implementation at the local level means that specific ecological, socioeconomic, and cultural conditions can be taken into account, they can also suffer from problems such as unequal power relations and conflicts of interest within the villages. This dissertation suggests that the latter problem may be particularly salient in villages, like Tomado, in the Lindu valley, where there exists considerable diversity in environmental ideologies and behavior within the "local community." The KKM meeting held in Tomado on Nov. 15, 2003 included members of the traditional village council and village government, all of whom except for one are indigenous Lindu people. This incomplete representation of the local community in Tomado may hinder the success of the institution, and therefore points to value of ethnography like that conducted in this dissertation in identifying where knowledge and attitudes regarding the National Park and conservation diverge within the community. If it indeed is the migrants who are responsible for all the damage to the forests of Lindu, as the Lindu people contend, then it is precisely these people whose environmental perceptions need to be understood and who need to be included in the conservation effort. A lack of understanding of "community" can result in projects that perpetuate or increase inequities (Brosius & Russell, 2003), but also can exclude resource users whose inclusion and participation may be critical for conservation action.

Summary

The approach used in this dissertation envisions human and nonhuman primates as members of a dynamic ecosystem when attempting to understand the ecological and behavioral plasticity of nonhuman primates that live in human-modified environments. This "human-nonhuman primate community" approach addresses both human and nonhuman primates' "perspectives" of overlapping habitat and resource use, thus necessitating the use and integration of theory and techniques from both biological and cultural anthropology. By doing so, it provides another way to bridge these seemingly disparate subfields of anthropology.

The research presented herein has shown that Tonkean macaques can adjust their diet, activity patterns, and ranging patterns in response to changes in their environment, and that this flexibility may allow them to persist in areas subject to human influence and use. These results point to the conservation value of human-modified landscapes, such as agroforests, for nonhuman primates and other forest dwellers. Important next steps towards the conservation of *Macaca tonkeana* might include (1) an investigation of the nutritional consequences of the observed foraging flexibility of Tonkean macaques by measuring feeding rate, as this can vary for different foods (Milton, 1984), nutrient intake, and the actual nutrient content of the food items consumed; (2) measuring the resources available in the intensively-used quadrats within the Anca group's range in order to further understand precisely what resources may be guiding their movement patterns and use of space; and, (3) an examination of the ability of Tonkean macaques to utilize habitats at higher elevations, given the fact that 90% of Lore Lindu National Park is comprised of montane forest ranging up to 2355 m in elevation and the conversion of lower elevation habitat to agricultural areas continues to increase in areas adjacent to and within the park (TNC, 2001).

Also exemplified by this dissertation is the value of ethnography in identifying the priorities and values of local communities regarding protected area conservation. I have explored both the active realm of human ecology (e.g., forest product use) and the conceptual realm (i.e., conceptualizations of the forest, wildlife, and the National Park), which together provide a more nuanced view of the ways villagers in Lindu interact with their environment. Given that conservation inherently involves the values and actions of humans, these data are also well suited to inform conservation action. For example, the finding that there is considerable diversity in environmental conceptualizations within the local community that vary by ethnic and religious background can better inform the implementation of collaborative community conservation such as the efforts initiated in Lore Lindu National Park; it may be insufficient and unproductive to only enlist official and traditional government members whose views may only represent a fraction of the community. Furthermore, it may be more appropriate for these locally-based efforts to concentrate on environmental problems that are a real concern to the community (e.g., prevention of floods, erosion, and landslides, and the protection of forest resources), which may act as more powerful incentives against forest degradation as opposed to the Western value of species preservation.

Since ethnoprimatology was first coined by Leslie Sponsel (1997), there has been a growing interest in this field of study as evidenced by two edited volumes[3] addressing the human-nonhuman primate interface, and a recent symposium, "The Human-Nonhuman Primate Interface: History, Evolution and Conservation," held at the 2005 meeting of the American Association of Physical Anthropologists[4]. By focusing on an interaction paradigm rather than a pristine paradigm, ethnoprimatology encompasses a flexible approach to the integration of the interests and concerns of both human and nonhuman primates (Fuentes & Wolfe, 2002). As such, ethnoprimatological research shows considerable potential to provide holistic solutions to very complex problems.

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[3] Fuentes & Wolfe, eds. (2002) "Primates Face to Face: Conservation Implications of Human-Nonhuman Primate Interconnections" and Paterson, ed. (in press) "Primate Commensalism and Conflict."

[4] The symposium was organized by Trudy Turner, Agustin Fuentes, and Fred Anapol.

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