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FOREST EDGE EFFECTS ON THE BEHAVIORAL ECOLOGY OF L'HOEST'S MONKEY (*Cercopithecus lhoesti*) IN BWINDI IMPENETRABLE NATIONAL PARK, UGANDA

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FOREST EDGE EFFECTS ON THE BEHAVIORAL ECOLOGY OF L'HOEST'S MONKEY (*Cercopithecus lhoesti*) IN BWINDI IMPENETRABLE NATIONAL PARK, UGANDA

by

Tharcisse Ukizintambara

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DEDICATION

For you mom and dad,

Astèrie Kanyonga

and

Jean de Dieu Muzigantambara

You have always been on my side and celebrated my achievements.

Dad, sit tibi terra levis.

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ABSTRACT

Forest edges are associated with forest edge effects that result from changes in physical features of the habitat, predator species and number, and prominence of human activities and other disturbances that can have direct or indirect impact on the distribution, ecology, and fitness of forest plant and animal species. I conducted a literature review on edge effects on primate species and came up with a classification of primate species in three general categories – thriving, sensitive and resilient species to edge effects – based on behavioral and demographic responses.

In Bwindi Impenetrable National Park, edge effects followed non-monotonic patterns (wave-like) most likely due to the additive influence of edge effects, the history of logging in the area, and the persistent human activities and other disturbances. Such edge effects were more detectable in vegetation canopy cover and density and distribution of pioneer plant species whose dominance could increase or decrease up to 400 m from the park boundary towards the interior of the forest. Such distance, however, can vary considerably depending on variables examined.

L'Hoest's monkeys living along the edge of the Bwindi forest did not appear to be more affected behaviorally by edge effects than an interior group. Both groups spent relatively equivalent amount of time on major behavioral activities such as feeding, travelling and resting. Socializing was significantly less in the edge group compared with the interior group and that is likely to have a detrimental effect on the edge group cohesion. A correlation was found between the abundance of plant food species and the amount of time l’Hoest’s monkeys spent feeding on these plant food species along the forest boundary while monkeys of the interior group fed on different items regardless of their abundance. The edge group had also a larger home range than the interior group especially because they expanded it during crop raiding or feeding on native vegetation in fallows outside the park.

Crop raiding was a very risky activity during which l’Hoest’s monkeys experienced fatal confrontations with local farmers. Although early work suggested that forest edges were beneficial to wildlife, this study has concluded that forest edges in Bwindi can be ecological traps or sink areas for the edge-resilient l’Hoest’s monkey species whose edge groups rely on immigration from the interior forest groups to survive and cope with disturbances and threats associated with forest edges.

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INTRODUCTION

This study examined the edge effects on the behavioral ecology of l'Hoest's monkeys (*Cercopithecus* lhoesti) in Bwindi Impenetrable National Park in Uganda. Edge effects are conditions that influence species distribution, richness, and behavior following complex causal mechanisms (Leopold, 1933; Odum, 1971; Laurance & Bierregaard, 1997; Foggo et al., 2001). These mechanisms, for example, comprise different ways in which species respond to variations in the intensity of abiotic factors (light, temperature, wind) and changes in abundance of biotic factors (food, predation, parasitism) as a function of the distance from the forest edges (Atkinson, 2003).

Edge effect studies on primate species behavior have so far received limited coverage. Most edge effect studies have assessed the densities of primate species in relation to forest boundaries (Mbora & Meikle, 2004; Tweheyo et al., 2004; Lehman et al., 2006a). According to Irwin (2008), censuses alone, if not conducted over time, may not be able to predict the long-term viability of species. However, census studies have recognized the usefulness of behavioral characteristics for interpreting patterns in spatial distribution data. Lehman et al.'s (2006b) classifications of how lemurs are distributed in relation to forest edges in Madagascar reflected at the same time the behavioral ecology and bio-geographical distribution of species. Lemurs were categorized into three broad categories: (1) "edge-tolerant" for species that have their highest densities near forest edges, (2) "edge-intolerant" for species that avoid forest edges, and (3) "omnipresent" representing species that show little or no response to edge and matrix conditions.

Long-term behavioral ecology studies are necessary for understanding the life of species on forest edges. Murcia (1995), Gordon et al. (1996), Treves (1999) and Lehman et al. (2006b) recognize that finding food and avoiding predators are two of the most important ecological demands that influence species distribution and survival. By optimizing feeding, primate species meet their nutritional requirement for survival, growth and reproduction. Evolutionarily, primates, compared with other animals, possess an advanced cognitive ability to process information on the amount, distribution, and quality of potential food items. There are temporal and spatial variations in the distribution of food and that of threats (Treves, 1999). While feeding especially on forest edges, primates must also scan the environment for competitors, predators, and other threats and disturbances (e.g. Illius & Fitzgibbon, 1994).

Edge habitats modified by anthropogenic activities may reduce or increase the opportunities of animal species to forage, disperse, or flee from predators (see Kunkel & Pletscher, 2000). Human activities affect the vegetation cover. Dense habitat may reduce predation rates by providing concealment and cover, thereby decreasing predation success (Gregg et al., 1994). Kunkel & Pletscher (2000) found that moose were more likely to be killed by wolves in more open habitats than in the dense interior vegetation of the North Fork Valley in British Columbia, Canada. Human presence and activities can also affect negatively the distribution of primates through habitat modifications or animal persecution (Goldstein & Richard, 1989; Richard et al. 1989). In the Bwindi forest in Uganda, due to the high frequency of human activities on the periphery of the forest, gorillas were more restricted to the interior of the park (Harcourt, 1981), while groups of baboons concentrated their foraging activities on the forest edge (Olupot, 2004).

The conservation of primate species living on forest edges will depend on how we understand evolutionary behavioral mechanisms that compel a species to avoid or thrive.

For forest primate populations to forage in habitats with less cover, they must find a trade-off between the energy gained from food and the energy lost while scanning for predators. Fitness would be compromised if predator scanning reduced the rates of feeding. This cost could be compensated by increasing foraging time, feeding in larger groups, or feeding in the most risk-free microhabitats (Illius & Fitzgibbon, 1994).

Increasing feeding time is an adjustment that conflicts with other activities such as socializing, resting, and vigilance. Living in large group sizes has been believed to reduce the individual vigilance “burden” as a “collective detection effect” (Lima, 1995). Nevertheless, if group sizes exceed a certain limit, individuals will be exposed to additional costs in the forms of breeding and feeding competition, or background noises that reduce sensory acuity in members and increase predation risks (Caine, 1984; Hardie & Buchanan-Smith, 1997; Treves, 1999; Roberts, 1999). Long-term research on species’ behavioral ecology may allow us to develop hypotheses about what, how much, and where primate species feed and how they organize their self-defense mechanisms in relation to “areas of tension” or “ecological traps” such as forest edges (Treves, 1999; Lehman et al., 2006b).

Butynski (1985) and McNeilage et al. (2001) found that the density of the near-threatened l’Hoest’s monkeys (IUCN, 2008) was higher on the edges than in the interior of Bwindi Impenetrable National Park. As such, l’Hoest’s monkey species could serve as an excellent model for investigating species survival strategies on forest edges. L’Hoest’s monkeys can be used to answer how a species balances the cost of foraging in presumably food-rich but hazardous edge microhabitats (see Fedigan & Fedigan, 1988; Yahner, 1988; Ferreira & Laurance, 1997; Irwin, 2008). The objectives of this dissertation research were twofold: (1) to examine the composition of edge and interior habitats in the Bwindi Impenetrable forest and (2) to determine how the ranging, foraging, and survival strategies of l'Hoest's monkeys have been fashioned by edge effects in the Bwindi forest.

Chapter 1 provides an overview of edge effect studies on biodiversity distribution and on the behavioral ecology of primate species living on the edges of tropical forests. I analyze the quality of forest edges and how primate species respond behaviorally to these edges. I highlight how forest edges can grant animal species access to diverse types of habitats and food items but also expose them to hazards and challenges. I describe how the forest edge effect theory has emerged from such a contradiction and how a unified applied science is surfacing from the edge effect theory.

Chapter 2 tests three hypotheses: whether (1) the distribution, abundance and richness of tree, shrub species and flowering plants, (2) the distribution and abundance of tree seedlings and terrestrial herbaceous vegetation and (3) the ground and canopy vegetation cover vary between the edge and the interior of Bwindi Impenetrable National Park in Uganda. Bwindi has been transformed into a forest island with seriously degraded forest edges surrounded by matrices of non-forest habitats. Human encroachment on the natural resources in Bwindi has also been extensive. As a result of edge effects and past anthropogenic activities characterized by heavy logging with pitsaws, the edges of Bwindi are expected to have differences in vegetation structure, composition and characteristics compared with the interior forest.

Chapter 3 examines whether (1) daily path lengths, (2) home range sizes, and (3) feeding time are different between the edge and the interior groups of l'Hoest's monkeys in Bwindi. Significant differences in ranging and foraging behaviors are expected between the edge and interior groups. Due to negative edge effects, the edge group may have longer daily paths and larger home range sizes but feed on a much more diverse diet, including local crops, than the interior group.

Chapter 4 studies how edge and interior group membership and behavioral activities may be differently influenced by edge disturbances. This chapter specifically assesses the negative impact that human encroachment, exposure to predation, and other edge-related threats and disturbances have on the survival of l'Hoest's monkeys on the edges of the Bwindi Impenetrable forest.

LITERATURE CITED

Atkinson P.I. 2003. *Edge effects and birds across karri forest (Eucalyptus diversicolor) clear-fell edges: A study of theory and conservation management*. Dissertation. University of Murdoch. Australia.

Butynski T.M. 1985. Primates and their conservation in the Impenetrable (Bwindi) Forest, Uganda. *Primate Conservation* 6: 63-72.

Caine N.G. 1984. Visual scanning by tamarins. A description of the behavior and tests of two derived hypotheses. *Folia Primatologica* 43: 59-67.

Fedigan L. & L.M. Fedigan. 1988. *Cercopithecus aethiops: a review of field studies*. In Gautier-Hion A., F. Bourlière & J.-P. Gautier (Eds.). *A primate radiation: evolutionary biology of the African guenons*. Cambridge University Press. Cambridge. pp. 389-411.

Ferreira L.V. & W.F. Laurance. 1997. Effects of forest fragmentation on mortality and damage of selected trees in central Amazonia. *Conservation Biology* 11: 797-801.

Foggo A., C.M.P. Ozanne, M.R. Speight & C. Hambler. 2001. Edge effects and tropical forest canopy invertebrates. *Plant Ecology* 153: 347-359.

Goldstein S.J. & A.F. Richard. 1989. Ecology of rhesus macaques (*Macaca mulata*) in Northwest Pakistan. *International Journal of Primatology* 10:531-567.

Gregg M. A., J. A. Crawford, M. S. Drut & A. K. Delong. 1994. Vegetational cover and predation of Sage Grouse nests in Oregon. *Journal of Wildlife Management* 58: 162-166.

Gordon I.J., A.W. Illius & J.D. Milne. 1996. Sources of variation in the foraging efficiency of grazing ruminants. *Functional Ecology* 10: 219-226.

Harcourt A.H. 1981. Can Uganda's gorillas survive? A survey of the Bwindi forest reserve. *Biological Conservation* 19: 269-282.

Hardie S.M. & H.M. Buchanan-Smith. 1997. Vigilance in single- and mixed-species groups of tamarins (*Saguinus labiatus* and *Saguinus fuscicollis*). *International Journal of Primatology* 18: 217-234.

Illius A.W. & C. Fitzgibbon, 1994. Costs of vigilance in foraging ungulates. *Animal Behavior* 47: 481-484.

Irwin M.T. 2008. Diademed sifaka (*Propithecus diadema*) ranging and habitat use in continuous and fragmented forest: higher density but lower viability in gragments? *Biotropica* 40: 231-240.

IUCN 2008. *2008 IUCN Red List of Threatened Species*. www.iucnredlist.org. Downloaded on 20 February 2009.

Kunkel K.E. & D.H. Pletscher. 2000. Habitat factors affecting vulnerability of moose to predation by wolves in southeastern British Columbia. *Canadian Journal of Zoology* 78: 150-157.

Lehman S.M., A. Rajaonson & S. Day. 2006a. Edge effects and their influence on lemur density and distribution in Southeast Madagascar. *American Journal of Physical Anthroplogy* 129: 232-241.

Lehman S.M., A. Rajaonson & S. Day. 2006b. Lemur responses to edge effects in the Vohobola III classified forest, Madagascar. *American Journal of Physical Anthroplogy* 68: 293-299.

Lima S. L. 1995. Back to basics of anti-predatory vigilance: The group size effect. *Animal Behavior* 49: 11-20.

Laurance W.F. & R.O. Bierregaard Jr. (Eds.). 1997. *Tropical forest remnants: ecology, management, and conservation of fragmented communities*. University of Chicago Press. Chicago.

Leopold A. 1933. *Game management*. Charles Scribner's Sons. New York.

Mbora D.N.M. & D.B. Meikle. 2004. Forest fragmentation and the distribution, abundance and conservation of the Tana River red colobus (*Procolobus rufimitratus*). *Biological Conservation* 118: 67-77.

McNeilage A., A.J. Plumptre, A. Brock-Doyle & A. Vedder. 2001. Bwindi Impenetrable National Park, Uganda: Gorilla census 1997. *Oryx* 35: 39-47.

Murcia C. 1995. Edge effect in fragmented forests: Implications for conservation. *Trends in Ecology & Evolution* 10: 58-62.

Odum E. 1971. *Fundamentals of Ecology*. W.B. Saunders Company. Philadelphia.

Olupot, W. 2004. *Boundary edge effects in Bwindi Impenetrable National Park*. Institute of Tropical Forest Conservation. Uganda.

Richard A.F., S.J. Goldstein & R.E. Dewar. 1989. Weed Macaques: The evolutionary implications of Macaques feeding ecology. *International Journal of Primatology* 10: 569-594.

Roberts G. 1999. Why individual vigilance declines as group size increases. *Animal Behavior* 51: 1077-1086.

Treves A. 1999. Within-group vigilance in red colobus and redtail monkeys. *American Journal of Primatology* 48: 113-126.

Tweheyo M., K.A. Lye & R.B. Weladjic. 2004. Chimpanzee diet and habitat selection in the Budongo Forest Reserve, Uganda. *Forest Ecology and Management* 188: 267-278.

Yahner R.H. 1988. Changes in wildlife communities near edges. *Conservation Biology* 2: 333-339.

CHAPTER 1

PRIMATE RESPONSES TO FOREST EDGES

ABSTRACT

High deforestation rates caused primarily by human activities in tropical landscapes have created a large number of forest fragments and increased the extent of forest edges. The impacts of these forest edges on species are not fully understood, but they are believed to have contrasting effects. Edges may (1) generate favorable conditions for certain species to proliferate and (2) at the same time increase pressures and risks to the extent that the populations of these species will decline or become locally extinct. In this chapter, I review how forest edges can serve either as rich areas for wildlife or as zones of unpredictable risk to wildlife populations. I focus on primate species because they are relatively large-bodied mammals that play a major role in ecosystem services, including seed dispersal, and they are important in tourism and revenue generation in tropical nations. Primates also manifest differential responses regarding forest edge effects according to their evolutionary history and adaptability, the nature of forest edges, and the structure of the surrounding landscape. 'Living on the edge' provides great opportunities for a species in terms of food and refuge from competition but forest edges have also conservation implications since they expose primate species to unprecedented risks such as predation, parasitism, increased mortality, or conflicts with humans. Therefore, I argue that we can best understand edge effects on primates by classifying primate species into three main categories: thriving, sensitive, or resilient to edge effects based on behavioral and demographic responses. An understanding of forest edge effect complexity – the foundation of the edge effect theory – is essential for developing a unified applied science on which to base effective conservation measures for all species living in forest edges and their habitats, particularly primate species living in tropical biodiversity hotspots. Edge effects will then be viewed as an ecological phenomenon that provides certain species with benefits *and* survival challenges which present conservation opportunities and challenges that forest managers will need to address when dealing with threatened, edge-sensitive and edge-resilient species.

Key words: Tropical forest edges, Edge effect theory, primate species responses, edge resilient species and conservation

INTRODUCTION

Habitat loss is one of the greatest obstacles to biodiversity conservation in the tropics (Noss, 1991; Newmark, 2001). The clear-cutting of forest for agricultural and development activities has isolated and compressed primate populations and other taxa into small island forests and exposed them to disturbances that characterize forest edges (Yahner, 1988; Onderdonk & Chapman, 2000; Siex, 2003). The majority of these populations might decline considerably and eventually become locally extinct. For example, over the last ten years, orangutan populations have declined by more than 30% due to forest clearing in Southeast Asia (van Schaik, 2004). Such forest loss has restricted and isolated populations of orangutans to remaining forest fragments and exposed them to harsh forest edge conditions on the islands of Borneo and Sumatra in the Indo-Malaysian region.

Early work by Leopold (1933) argued that forest edges could provide great opportunities for animal species to flourish; more recently, research has shown that edges can expose species to unpredictable risks (Didham et al., 1998; Gillespie & Chapman, 2006; Irwin, 2008). In this review, I discuss how responses of primate species to edge effects vary according to their evolutionary history and adaptability, the nature of forest edges, the structure of surrounding landscape (matrix effects, see Gascon et al., 1999; Dauber et al., 2003), and the effects of local interactions among landscapes, plant and animal species, and human beings.

The objective of this review is to illustrate differential responses of primate species to forest edge effects. Primates are our closest relatives (Mittermeier, 1997), and studying their behavioral ecology will advance the understanding of human evolution and survival. Primatological research also provides relevant information to tropical ecology and conservation, as primates play a vital role in the dynamics of tropical forests as seed dispersers, seed predators, and even pollinators (Terborgh, 1983; Tutin et al., 1991). Primates have also become important components of ecotourism-linked conservation efforts (Butynski & Kalina, 1998).

In this chapter, I analyze direct and indirect effects of tropical forest loss on plant and animal species in general and examine the physiognomy of forest edges and their effects on primate species particularly. I also define concepts, terms, and theories to put the forest edge effect theory into a broader context. I argue that primate species can be classified into three main categories –thriving, sensitive, or resilient – in relation to how they respond to forest edge effects. I especially emphasize case studies of edge-resilient primate species, which can be defined as primate populations that are able to cope with disturbance or perturbation (Wilson et al. 2008); these species are, however, not invulnerable to forest edge disturbances and require high population growth and recruitment rates because their survivorship in forest edges might be poor (see Done, 1987). These species can utilize both natural habitat and the perceived hostile environment offered by an adjacent matrix (Major et al. 2001). However, edge resilient species should be distinguished from edge specialists that are usually more abundant along forest edges than in the interior (Davies et al., 2000; Hooks et al., 2003; Christie & Hochuli, 2009). Edge-resilient species can be used to develop a unified applied science based on forest edge effect theory. Such science will encompass both beneficial and detrimental attributes that affect the survival of primate species and other taxa living on the forest edge and that make the conservation of threatened edge habitats a challenge.

BACKGROUND

Tropical forest deforestation

Deforestation has converted large continuous forests into many smaller and isolated forest fragments surrounded by non-forest matrix (Wilcove et al., 1986; Newmark, 2001). Direct effects of deforestation account for the amount of habitat loss that occurs simultaneously with the felling of trees (van der Laan & Petersen, 2005) and the creation of forest fragments characterized by extensive edges (Williams-Linera, 1990). Deforestation not only reduces the extent of forested areas, but also changes the shape and structure of the interface between the forest and surrounding matrix (Murcia, 1995). Deforestation also lowers species numbers and modifies community composition within remaining fragments (Turner, 1996). Over the last centuries, deforestation has reached alarming rates (Hartshorn, 1989; Turner, 1996). Approximately 125,000 km^2 of forests have been cleared each year (Chapman & Peres, 2001), making fragmented landscapes and edge-affected forest one of the most widespread features on earth, especially in the tropics (Williams-Linera, 1990; Achard et al., 2002; Laurance, 2003).

According to the area effect, as forest areas are reduced due to clearing for agriculture and development of industries and urban centers, the number of species also decreases. Small areas support only small populations, which are more sensitive to demographic fluctuations and stochastic perturbations (Pimm et al., 1988). Additionally, small areas are exposed to higher extinction rates: tiny relict patches may contain ‘ecologically extinct’ populations of species doomed because of their small numbers and isolation, increased probability of genetic drift, inbreeding, homozygosity, and decreased fitness.

Species richness is also negatively related to isolation (MacArthur & Wilson, 1967). Isolation effects result in further species loss, especially for nomadic and seasonally migrant forest animal species that disperse among forest fragments. For example, if animal species are unable to cross open areas, their home ranges will diminish and their population will decline following the isolation phenomenon known as ‘faunal relaxation’ (Whittaker, 1998). The survival of large carnivores, for example, depends on enhanced possibilities of immigration and emigration (Woodroffe & Ginsberg, 1998). Isolation also affects many plant species which require animals for the dispersal and regeneration of their seeds (Harvey, 2000; Cordeiro & Howe, 2001). Therefore, edge size, structure, and contrast (Figures 1 & 2) are considered the most important characteristics of forest edges that influence species diversity and richness. The fragmentation of large areas of forest into small fragments also exposes species to other edge phenomena, such as predation, parasitism, diseases, and increased mortality rates.

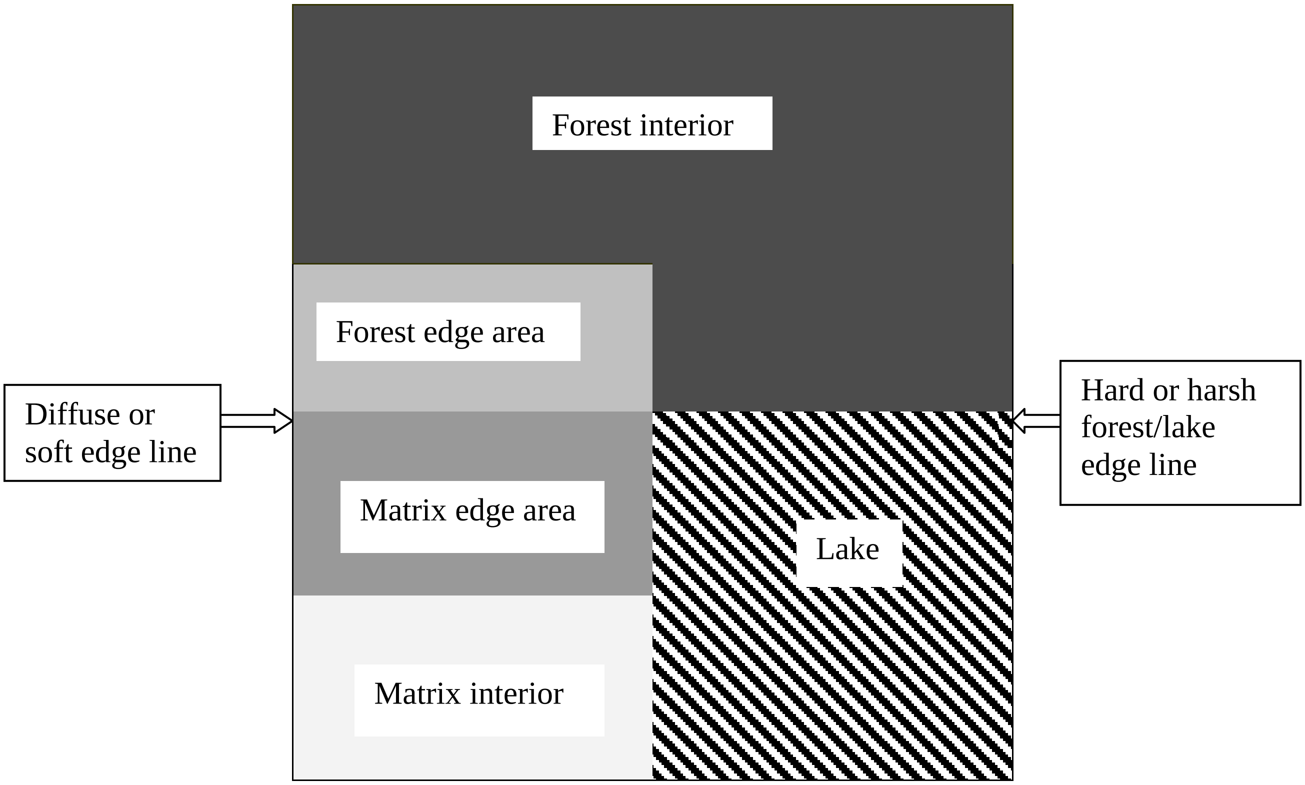

Figure 1. Spatial illustration of soft and hard edges between forest and an abandoned farmland matrix and between forest and lake (Adapted from Forman, 1995).

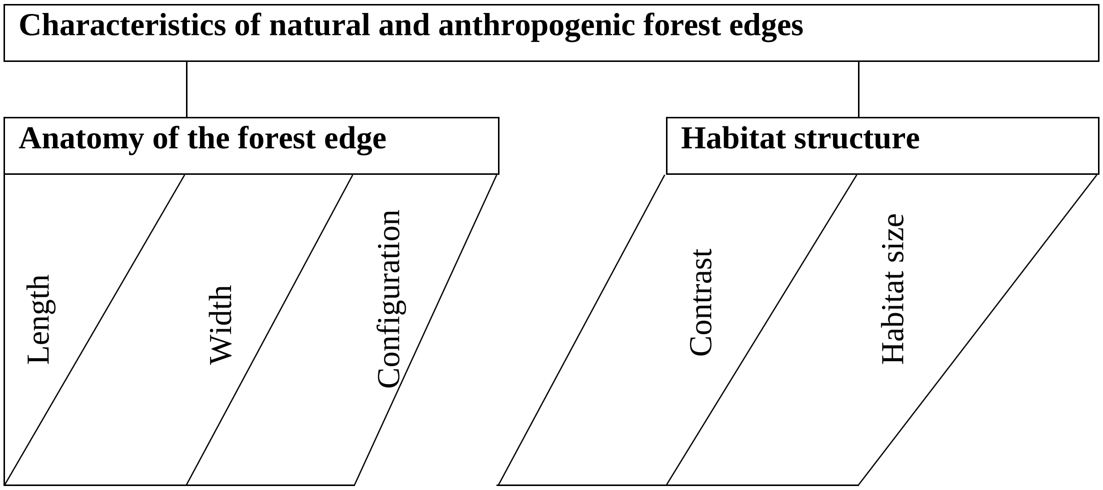

Figure 2. Characteristics of forest edges that influence habitat and species richness (Adapted from Thomas et al., 1979).

Forest edge effects

Forest edges are distinct and common components of the global landscape (Williams-Linera, 1990). Based on how they were formed, two types of edges or transitional zones between two habitats can be recognized: (1) Natural or inherent edges are long-term features located between two habitat types that have been demarcated by local differences in soil topography, hydrology, geomorphology, microclimate and microhabitat types (Thomas et al., 1979); (2) Induced or human-made edges are at the border between distinct land use types or management practices, such as between intact forest and landscapes used for grazing, logging, or farming (Yahner, 1988).

Forest edges can also be subdivided into two morphological types: (1) a sharp, hard or narrow edge with a well-defined boundary, such as the edge between a river and riverbank vegetation or between cultivated fields (e.g. of tea, maize, beans, etc.) and the forest, and (2) a diffuse, soft, or gradual formation of different plant communities known as ecotone (Yahner, 1988) (Figures 1, 2 and 3). Both sharp and diffuse edges are characterized by harsh and soft edge effects respectively, depending on the degree of effect on the forest edge (Gascon et al., 2000).

Tropical forests have been referred to as ‘jungles’ or impenetrable forests with a thick ‘wall’ of vegetation at the edge (Newman, 1990; Whittaker, 1998; Didham & Lawton, 1999; Hamberg et al., 2009). Along the forest edge, an impassable solid mass of towering vegetation can make an outside barrier, known as the “wall effect” (Hamberg et al., 2009). The wall is often compacted with a tangle of light-tolerant vines and climbers from which it would be assumed that the interior is just as dense (Newman, 1990). Matlack (1994) described a scenario in which edge-oriented effects arise very quickly in vegetation structure at newly formed edges due to abrupt changes in the microclimate gradient after deforestation. After 20 to 30 years, the canopy closes and canopy species return to their original abundance, while edge effects remain apparent within the understory vegetation and influence the distribution of semi-terrestrial herbivorous species, including primates.

Figure 3. Picture of a hard edge between a tropical montane forest (Bwindi Impenetrable National Forest) and surrounding farmlands in Uganda. © T. Ukizintambara

Forest edges have been viewed as areas of high plant, mammal, bird, and invertebrate species richness, density, and biomass (Forman, 1995; Sisk et al., 1997; Wolff et al., 1997; Foggo et al., 2001). However, the distribution and productivity of these species are affected by indirect edge effects operating through interspecies interactions and variable microclimatic or environmental conditions (Strauss, 1991) and different matrix or surrounding land use types. Kapos et al. (1997) reported high productivity in the flowers and fruits of edge and light-loving plant species that attract high densities of pollinator, frugivore, and seed-disperser species (Table 1). Leopold (1933) and Whittaker (1998) noticed an increase in numbers of certain species on the edges of forest reserves surrounded by non-forested matrices.

Table 1. Factors determining edge-related changes.
(Adapted from Lovejoy et al., 1986, p. 283 and Whittaker, 1998, p. 208).

Factor		**Description of change**	**Examples**	**Reference**
Abiotic		Increased	Temperature Light penetration Wind intensity	Matlack (1994) Kapos et al. (1997) Lovejoy et al. (1986)
		Decreased	Relative humidity	Williams-Linera (1990)
Biotic	First order	Increased	Tree mortality	Lovejoy et al. (1986)
			Tree falls on windward margin	Mesquita et al. (1999)
			Leaf fall	Matlack (1994) Williams-Linera (1990)
			Plant growth near margins	
		Decreased	Bird populations near margins	Stouffer & Bierregaard (1995)
	Second order	Increased	Light-loving insects (e.g. butterflies)	Bellinger et al. (1989)
	Third order	Decreased	Forest interior butterflies	Bellinger et al. (1989)
		Enhanced	Survival of insectivorous species (e.g. lion tamarins)	Lovejoy et al. (1986)

Effects of forest edges

After pioneer plants and secondary vegetation establish at forest edges, they produce abundant leaves, which often have less chemical defense than plants growing in mature interior forests (Arnold & Schultz, 2002). In addition, most of these pioneer species are sources of leaves and abundant fruits with small-sized seeds that attract many animal species, from herbivores, including high densities of arthropods and herbivorous insects, to insectivorous and frugivorous birds and mammals, including birds and some primate species, and ultimately their predators (McClanahan & Wolfe, 1993; Fimbel, 1994; Laurance, 2004; de Melo et al., 2006).

This edge recruitment of plants, insects, and mammals increases species diversity and abundance on forest edges (Leopold, 1933; Odum, 1971; Yahner, 1988; Whittaker, 1998). From these observations, the creation of more forest edges was recommended by many early wildlife managers to improve habitat quality (Leopold, 1933; Yahner, 1988; Paton, 1994; Murcia, 1995; Foggo et al., 2001). May (1982) and Fagan et al. (2003) hypothesized that edge species have adapted to such conditions by developing generalist behaviors and capitalizing on food resources from adjacent and different ecosystems. This type of edge effect became an accepted paradigm in wildlife management (Reese & Ratti, 1988).

However, Newman (1990) and Whittaker (1998) have argued that the edge effect is “deceptive” because many edge species can be slowly wiped out by various threats associated with forest edges and edge effects. As fragmented landscapes have increased both the prominence and the proportion of edge areas, some ecologists from as early as the beginning of the 20th century started acknowledging the magnitude of ecological biases and negative effects of forest edges (Murcia, 1995). Scientists have understood that edge effects are factors that control ecological processes, including community structure and composition of forest boundaries (Lovejoy et al., 1986). These changes may coincide with a decline in population sizes of species that could be relatively stable in interior forest blocks (Ambuel & Temple, 1983). Many factors are responsible for the decline in populations of species living in forest edge habitats. These factors include: changes in forest microclimate and pressures from hunting and predation. These factors vary in relation to distance from the periphery towards the interior forest. The distance that edge effects penetrate into the forest varies from a few meters to 1 km or more depending on forest types, the nature of surrounding matrices, the edge effects studied, and the species studied (Turner, 1996; Whittaker, 1998; Curran et al., 1999; Olupot, 2004; Broadbent et al., 2008).

One of the most compelling pieces of evidence for population decline due to edge effects involves nest predation in avian communities (Paton, 1994; Andrén, 1995). The detection of negative edge-related patterns in bird nest predation has helped scientists to correct the early perception that forest edges were generally characterized by abundant and healthy wildlife populations (Sisk & Margules, 1993). Currently scientists know that species can respond either negatively or positively to forest edge effects.

Species responses to forest edges

As demonstrated above, there have been complications in interpreting edge effects (Laurance & Yansen, 1991). Some researchers have attributed to edge effects the role of boosting species abundance and diversity, while others described negative edge effects on species distribution, behavior, and survival (Yahner, 1988). To avoid this ambiguity, Atkinson (2003) coined the term ‘edge responses’ to characterize the reaction of a community, guild, or species to forest edges. Forest edges operate as a filter: they can grant certain species access to diverse types of habitats and food items and, at the same time, expose them to hazards and challenges (Reese & Ratti, 1988; Weiner, 1995). The survival of species depends on how effectively and quickly they adapt to such contrasting edge effects.

Most anthropogenic edges have been created through deforestation over the last centuries and have coincided with the extinction of numerous species (Swihart et al., 2003). Within this short (in geological time) ‘anthropocene’ period (Sanderson et al., 2002), species have developed one of three types of responses: 1) thriving, 2) sensitive, and 3) resilient towards edge effects (Didham et al., 1998; Lehman et al., 2006; Christie & Hochuli, 2009). The sensitivity or response of species to edges is related to several factors. The ability of a species to persist in forest edges depends on successfully adjusting its intrinsic ecological and behavioral characteristics to changes in abiotic factors such as light, temperature, and wind (Vos et al., 2001) and other extrinsic factors, including interspecific competition, predation, parasitism, and anthropogenic influences (Mönkkönene & Reunanen, 1999). This adjustment is species-specific and varies in time and space.

RESPONSES OF PRIMATE SPECIES TO EDGE EFFECTS

Primates respond differently to edge and disturbed zones, depending on the evolutionary history and characteristics of each species, as is the case for most taxonomic groups. Within a single species, primates may also vary in response to edges when studied in different locations, time periods or seasons. For instance, Fimbel (1994) observed higher densities of *Cercopithecus* spp. in disturbed forest edges and forest clearings where fruits were more abundant than in the interior of the Tiwai forest in Sierra Leone during the dry season. Gathua (2000) demonstrated seasonal variation in the ranging behavior of two neighbor groups of redtail monkeys (*Cercopithecus ascanius*) in the Kakamega forest in Kenya. The forest interior group had a larger monthly and annual home range area and traveled farther than the edge group to maintain a higher percentage of fruit intake. Gathua (2000) speculated that this pattern was a result of the lower density and sparse distribution of fruits eaten by redtail monkeys inside the Kakamega forest.

Sisk & Margules (1993) and Sisk et al. (1997) developed a complex array of potential responses by bird species to habitat types, including forest edges. They described edge avoidance, edge preference, neutral response, preference for mature forest, preference for established regrowth, and preference for both juvenile regrowth and mature forest. In this literature review, for the purpose of simplicity and clarity, I have synthesized published examples of edge responses by primates to create three edge response categories for primates (sensu McIntyre & Barrett, 1992 and adapted from Lehman et al., 2006): (1) thriving species that are well adapted to the edge and can maintain populations along the edge without reliance on immigration from non-edge populations, (2) sensitive species that avoid the edge, and (3) resilient species that are able to cope with edge effects by relying on non-edge populations for immigration (Figure 4, adapted from Andrén, 1995). These categories portray the behavioral responses of primate species to edges, rather than simply depicting the notion of spatial distribution resulting from censuses (Lehman et al., 2006). Censuses are very important, but if not repeated over time, they may overlook the viability of populations (Twinomugisha, 2007; Irwin, 2008).

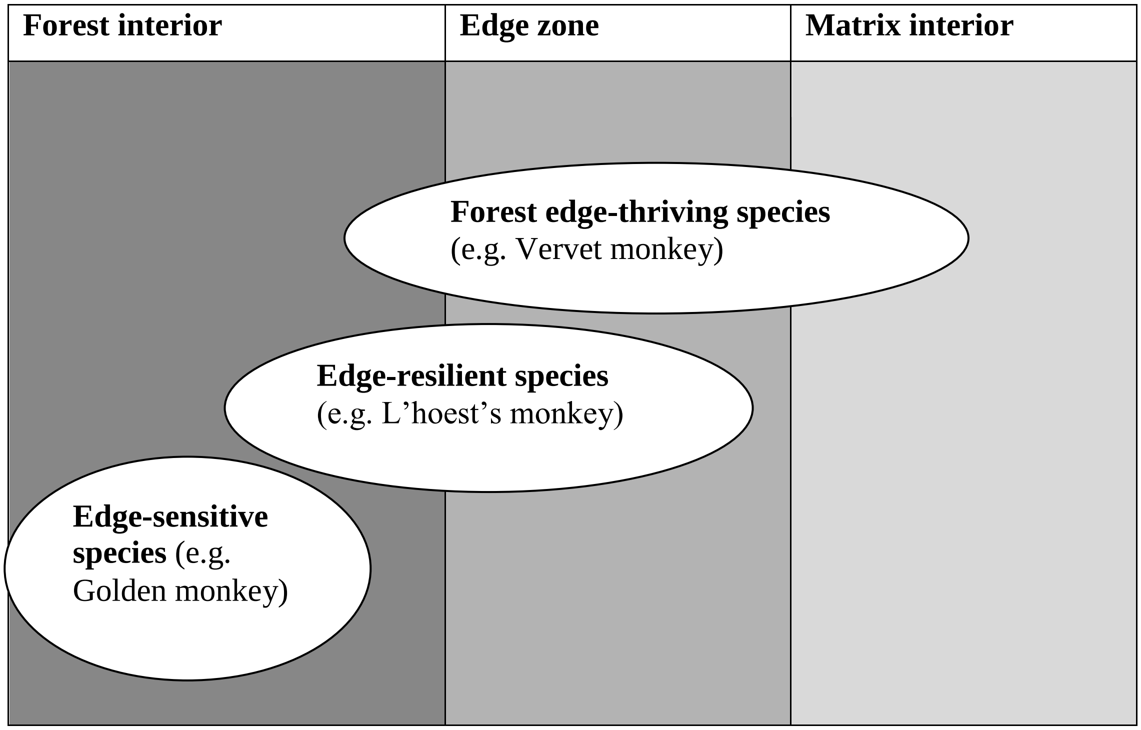

Figure 4. Theoretical distribution of primate species according to their responses to forest edge.

Forest edge thriving primate species

This category comprises primate species whose evolutionary history has helped them adapt to edge habitats and the conditions of forest edges. They range mostly on the periphery and in matrices outside the forest. The Old World primate taxa especially provide several examples, such as the vervet monkey (*Chlorocebus aethiops*), one of the species that best represents this category. Vervet monkeys have a mean home range size of 42 ha and female body weight of 5.6 kg (Ukizintambara & Thébaud, 2002). Vervet monkeys are distributed across sub-Saharan Africa, excluding most parts of the Congo Basin forest. They are also abundant in the Caribbean Islands of St. Kitts, Nevis, and

Barbados, where they were introduced and have successfully colonized (Fedigan & Fedigan, 1988). Other examples include the rhesus macaques (*Macaca mulata*) that have adapted to open habitats and feed in heavily disturbed parts of forest mosaics in Pakistan (Richard et al., 1989) and baboons that use the near edge zone and raid neighboring maize and millet crops in the Bwindi Impenetrable Forest in Uganda (Olupot, 2004).

The successful distribution of primate species such as vervets, macaques, and baboons on forest edges relates to their extraordinary flexibility and opportunistic behavior. They are among the few primate species that prefer forest edges and thrive where humans convert forests and savannah woodlands into agricultural lands, pastures, and urban settlements. Brennan et al. (1985) reported that vervet densities were higher near tourists' lodges than elsewhere in Amboseli National Park in Kenya. Relatively large populations of vervet monkeys can also be found in the vicinity of large settlements in Africa, including some of the suburbs of metropolitan Nairobi. In the islands of West Indies, introduced populations of vervets remain large in spite of high persecution, hunting, and trapping by humans for laboratory demands.

By adapting to novel habitats, edge-thriving species have developed unique behaviors. While crop raiding, for example, vervet monkeys cease to give loud calls but emit less locatable communication sounds and post on tallest edge trees a "sentinel" that warns them of any danger (Fedigan & Fedigan, 1988). This sophisticated behavior is also found among other widely distributed semi-terrestrial primates such as macaques and baboons, which are also well adapted to edge, transitional, and disturbed habitats. In such crop-raiding species, significant changes in diet have also been observed. Gautier-Hion (1988) found that cassava, a crop that was introduced in Africa only in the 19th century, made up 17% of the diet of the northern talapoin monkeys (*Miopithecus ogouensis*) in Gabon. Indeed, most edge-thriving primate species, including vervets, baboons, and macaques, raid crops regularly or depend on provisioning and stealing food from human settlements. In many places, these species have been referred to as 'house sparrows' (Fedigan & Fedigan, 1988, p. 411), 'weed species' (Richard et al., 1989), or pest and vermin species (Fimbel, 1994).

As the area of anthropogenic edge-affected forests increases, certain populations could decline due to third order effects (Lovejoy et al., 1986, Table 1). The transmission of diseases from human to edge species or from edge species to interior species (Crooks, 2002; Chapman et al., 2006) is an example. In the Bwindi forest, Uganda, large groups of baboons spend a great amount of time in forest edges and invade local farms (Olupot, 2004). They are considered pest species by the local inhabitants, some of whom believe they should be eradicated (Baker, 2004; Andama, 2007). Conservationists are concerned about baboons and other pest species that raid local farmers' crops and transmit diseases from humans to endangered gorillas following higher order and edge effects (Hope et al., 2004; Köndgen et al., 2008).

Edge-sensitive primates

Edge-sensitive species are intolerant to changes and disturbances associated with edge-affected forest. Among the Old World monkeys, the apparent reluctance of Samango (*Cercopithecus mitis labiatus*) and golden monkeys (*Cercopithecus mitis kandti*), both subspecies of *Cercopithecus mitis,* to disperse in disturbed habitats and forest fragments may be an indication that they avoid forest edges (Lawes, 2002; Twinomugisha, 2007). Lawes (2002) discussed the importance of fragment size for

Samango monkeys, but a combination of life-history traits, social structure, dietary flexibility, the structure of edge forest, and the nature of surrounding matrices may prevent from ranging in forest edges but does not explain how the. Twinomugisha (2007) found that the golden monkey avoids disturbed, low-quality habitats and open areas, apparently to minimize costs of foraging, vigilance, and thermoregulation, and can be considered a forest specialist species. When edge-sensitive species persist in fragmented habitats, it can be indicative of the good health and integrity of the entire ecosystem (Noss, 1991). According to Soulé and Terborgh (1999), edge sensitive primates can therefore be used to assess subtle ecological disturbances in protected forests.

Edge-resilient primates

Edge-resilience is the ability to withstand edge effects and edge-related threats and is determined by several factors, including dietary flexibility and foraging behavior (Atkinson, 2003). Although not invulnerable, edge-resilient species can cope with edge disturbances, and their survivorship on the edge depends on immigration from interior forest groups and high recruitment rates compared with species that avoid edge habitats (Done, 1987; Wilson et al., 2008). Food is the number one factor in explaining why some forest-dwelling monkeys frequent open disturbed habitats, secondary growth, and forest edges and farmlands (Butynski, 1985; Gautier-Hion, 1988; Naughton-Treves et al., 1998; Kaplin & Moermond, 2000). Edge-resilient primate species include those that have adapted to foraging in secondary habitats and gaps within contiguous forest (i.e. regrowth area, streamsides, and treefalls) (Marsh, 2003).

Many primate species can persist on forest edges due to their generalist or flexible feeding behavior. In the neotropics, golden-handed tamarins (*Saguinus midas*), for example, are small frugivorous-insectivorous primates living in small groups (4-10 individuals) typically in medium sized home ranges (10-30 ha). They range most commonly in dense vegetation mixed with tall primary forest and secondary growth such as along margins of streams and swamps and in gaps created by treefalls and on forest edges. Highly clumped edge plant species produce small fruits of low yield that are insignificant to large primate species but attract small primates such as marmosets and tamarins because of their prolonged production season in the Neotropics (Terborgh, 1983). Red howler monkeys (*Alouatta seniculus*) found in Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Peru, Suriname, and Venezuela also live in small groups (3-10 individuals) and occupy a small home range (3-7 ha). They are the most folivorous of the neotropical primates. They forage on forest edges where leaves are most abundant (Lovejoy et al., 1986; Chapman & Balcomb, 1998; Fedigan & Jack. 2001). White-faced sakis (*Pithecia pithecia*), found in Brazil, French Guiana, Guyana, Suriname, and Venezuela, occupy and defend small home ranges of 10ha or less. Their group size varies between 2 and 5 individuals. Very little is known about this species, but it is believed to thrive on forest edges and in areas where secondary growth predominates (Lovejoy et al., 1986; Schwarzkopf & Rylands, 1989).

In tropical Africa, l'Hoest's monkeys (*Cercopithecus lhoesti*) could be considered an edge-resilient species. L'Hoest's monkey is a semi-terrestrial species whose group size can vary from a few to over 40 individuals, daily path lengths from 1100 m to 2500 m, and home ranges from 30 ha to 85 ha (Kingdon, 1997; Kaplin and Moermond, 2000; Tashiro, 2005; Ukizintambara, unpublished data). They are believed to tolerate human-induced disturbances and forest edges (Butynski, 1985; Johns & Skorupa, 1987; Kaplin and Moermond, 2000; McNeilage et al., 2001) in Uganda and Rwanda. They are fond of terrestrial herbaceous vegetation (THV) and insects that they find mainly in undisturbed forest but also in disturbed forest, forest gaps, and edges (Kaplin, 2002; Tashiro, 2005). As forest-adapted species, l'Hoest's monkeys spend a considerable amount of time in early successional growth and use forest edges to access abundant food resources (Kaplin and Moermond 2000; Ukizintambara, unpublished data).

Resilience may be observed in some aspect of adaptation to forest edge conditions. According to Done (1987) and Owen-Smith (1990), as a population becomes more sensitive to localized sources of mortality, it may also become resilient in the sense of increasing growth rates or survivorship that promote recovery from disturbance. For example, due to the high risk of being exposed to predation and persecution on the edge and outside the park, l'Hoest's monkeys appear to be wary, and will only venture out of the forest to feed on native species found in the fallows and on novel items, mostly farmers' crops or other introduced species, such as the seed of the Australian black wattle tree (*Acacia mearnsii*, Leguminosae), after making sure that it is safe to go outside. Hesitant juvenile l'Hoest's monkeys remain behind in tall trees at the forest edge and will alert crop-raiders, mostly adults, in case of danger (Ukizintambara, unpublished data). This behavior is very similar to that of edge-thriving vervet monkeys as it was described by Fedigan & Fedigan (1988).

Primate species can also respond to intense edge threats by increasing rates of reproduction, resulting in large group sizes, which allows individuals to reduce time spent being vigilant, especially in open habitats (Illius & Fitzgibbon, 1994), thus offering greater time for foraging. In the Bwindi forest in Uganda, Ukizintambara (unpublished data) documented that after one year the edge group size had declined by over 20% due to eagle attacks, infanticide, and human persecution. By comparison, only two casualties due to apparent natural causes were recorded in the interior group. However, Ukizintambara (unpublished data) also observed that the edge groups of l'Hoest's monkeys were larger compared to the interior forest groups, and this pattern could be associated with relatively higher birth and immigration rates in edge groups compared to interior forest groups, a resilience strategy that l'Hoest's monkeys could have acquired to cope with edge disturbances (Wilson et al., 2008).

EDGE EFFECT THEORY: A UNIFIED APPLIED SCIENCE

Edge effect studies have led to the development of the "edge effect concept" or theory (Odum, 1971, p. 414), and edge effects are considered causal mechanisms influencing responses such as behavior, distribution, and abundance of species at the forest edge (Foggo et al., 2001). The edge effect theory is believed to cover areas that the celebrated island biogeography theory (MacArthur & Wilson, 1967) has been unable to cover (Laurance, 2008).

Many scientists have recognized the bias toward a positive view of edge effects and have called for a standardized protocol for measuring and comparing edge effects in different landscapes (Yahner, 1988; Murcia, 1995; Whittaker, 1998). Considering the relevance and importance of edge habitats and edge effects to ecological theories on habitat fragmentation, and to habitat management, more long-term studies are needed to assign rigorous management plans for forest edge areas and edge species (Reese & Ratti, 1988).

The fragmentation of forest reduces forest area, isolates remaining forest fragments and brings wildlife into closer proximity to humans. Interactions between wildlife and human communities have attracted much attention even outside the arena of natural sciences. Anthropological, ethnographic, socio-economic and political studies need a solid understanding of the natural history of species living on forest edges in order to mediate conflicts between human land uses and wildlife foraging behavior in forest fragment edges and non-forest matrices. Primates play an important role in forest ecological processes as pollinators and seed dispersers (Terborgh, 1983; Tutin et al., 1991). Although they raid crops along forest edges, primates have become important components of ecotourism-linked conservation efforts (Butynski & Kalina, 1998). So far, few empirical studies have examined different ecological edge effects on primates. Due to increasing forest edge areas, I believe that edge effect theory should be, as Forman (1995, p. 114) points out, “a frontier area for research” and a unified applied science in tropical ecology and conservation.

CONSERVATION OF PRIMATES SPECIES LIVING ON FOREST EDGES

Conservation efforts and land management practices should take into consideration the impacts of forest edges on biodiversity. Effective primate conservation requires an understanding of natural history and the effects of edges on primate populations. Understanding distinctions between edge-sensitive, edge-resilient and edge-thriving primate species is a key component in effective conservation efforts. For example, census data have estimated that l’Hoest’s monkeys may be abundant on forest edges of the Bwindi forest in Uganda (McNeilage et al., 2001), yet a behavioral study of one edge group of l’Hoest’s monkeys showed that its group size had declined by over

20% within one year (Ukizintambara, unpublished data). According to Irwin (2008), census data alone cannot depict when a disturbed edge forest becomes a species demographic sink. Increases in group sizes or population densities along edges may coincide with signs of stress which would ultimately jeopardize the long-term survival of a primate species (Irwin, 2008). Reducing the 'hardness' of edges may be one of the more effective conservation approaches in tropical forests today, where edge forests and edge effects are so common.

Edges are zones of tension between primate populations and the surrounding human-dominated landscape. Most conflicts between human and non-human primates and casualties happen in the agricultural matrix (Baker, 2004; Andama, 2007; Ukizintambara, unpublished data). The succession of disease transmission from humans to edge-thriving, to edge-resilient, and to edge-sensitive species is of great conservation concern (Chapman et al., 2006). In Bwindi, conservationists are trying to contain problem animals within the park by planting certain species, such as Mauritius thorn (*Artemisia annua*) and tea, or by establishing pasture grass in the buffer zone (Andama, 2007). Creating buffer zones is an example of a land use practice that can mitigate conflicts between humans and wildlife (Naughton-Treves, 1996). Buffer zones may extend from a few meters to kilometers along core protected areas (Andama, 2007). In the short-term, these buffers may be effective in creating soft edges, depending on their composition, despite the problem of land scarcity and land use around the park (Andama, 2007). The long-tem success of buffer zones will depend on the cooperation of farmers regarding which crops they will choose to grow and their decisions on the size of the buffer.

CONCLUSION

Information on edge effects and the natural history of primate species living on forest edges is still in an infancy stage. Yet rates of tropical deforestation remain high, along with rates of conversion of once interior forest to edge-affected forest. By promoting research on edge effects and on those species able to persist on the forest edge, scientists provide valuable information to conservation decision-makers for the protection of species and habitats. Although early work suggested that forest edges were beneficial to wildlife, we now recognize that edges can be ecological trap or species sink areas where edge-resilient species rely on immigration from the interior forest to cope with threats associated with forest edges. Research has led to the recognition of a distinction between edge and interior species, and discrepancies have also been shown between edge species depending on the characteristics of the edges and surrounding matrices (Yahner & Malan, 1997).

Currently, forest edges are rapidly becoming quantitatively important in tropical landscapes and this growth has far outpaced scientific advances and our understanding of processes associated with forest edges. Impressive and complex processes that characterize edge effects have often made comparisons across edge studies difficult because of differences in spatio-temporal scales, species studied, and research designs. In this review, I have suggested a framework for understanding primate response to edges using three categories: thriving, sensitive, or resilient to edge effects. At present, the edge effect theory recognizes that ‘living on the edge’ could provide great opportunities for a species in terms of food and refuge from competition, but edges also expose species to unprecedented risks such as predation, parasitism, increased mortality, or conflicts with humans.

The aim of this review is to differentiate responses of primate species to forest edge effects according to landscape and species characteristics and local circumstances, and to invite ecologists to develop rigorous methods for detecting the extent of forest edge areas and analyzing their effects on animal populations (see Olupot, 2009). Further progress will require improved collaboration and sustained efforts so that in the near term a united understanding of edge effect theory and an ability to predict the result of edge effects on primate species can be reached. Edge effects will then be viewed as an ecological opportunity that provides certain species with benefits *and* survival challenges, and also a conservation challenge that needs to be addressed when managing threatened, edge-sensitive and edge-sensitive species.

Edge-resilient species may be viewed as ecological models to assess habitat-species interaction hypotheses. Studying such models may provide evidence to support stabilization of the landscape matrix surrounding remaining fragmented forests, and especially the increasing edges. By conserving or stabilizing forest edges through encouraging the creation of soft edges, we may ensure the protection of interior forest habitats together with edge-resilient and edge-sensitive species at a low cost (see McIntyre & Barrett, 1992 and McIntyre & Hobbs, 1999). More long-term research on the nature of fragmentation, types of forest edges and surrounding matrices, edge effects, population dynamics of species living along edges, and species adaptation to forest edge disturbances is crucial to the advancement of science and the survival of primates and other animal and plant species living in disturbed forest edge zones.

LITERATURE CITED

Achard F., H.D. Eva, H.J. Stibig, P. Mayaux, J. Gallego, T. Richards & J.P. Malingreau. 2002. Determination of deforestation rates of the world's humid tropical forests. *Science* 297: 999-1002.

Ambuel B. & S.A. Temple. 1983. Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. *Ecology* 64: 1057-1068.

Andama E. 2007. *Invasive potential of Mauritius thorn (Cesalpinia decapetala) (Roth) Alston and its use to deter crop raiding by wild animals around Bwindi Impenetrable National Park, Uganda*. Dissertation. Makerere University.

Andrén H. 1995. *Effects of landscape composition on predation rates at habitat edges*. In Janson L., L. Fahrig & G. Merriam (Eds.). *Landscapes and Ecological Processes.* Chapman and Hall. London. Pp. 225-255.

Arnold T.M. & J.C. Schultz. 2002. Induced sink strength as a prerequisite for tannin biosynthesis in Populus. *Oecologia* 130: 585-593.

Atkinson P.I. 2003. *Edge effects and birds across karri forest (Eucalyptus diversicolor) clear-fell edges: A study of theory and conservation management*. Dissertation. University of Murdoch. Australia.

Baker J. 2004. *Evaluating conservation policy: Integrated conservation and development in Bwindi Impenetrable National Park, Uganda*. Dissertation. University of Kent. UK.

Bellinger R.G., F.W. Ravlin & M.L. McManus. 1989. Forest edge effects and their influence on gyspy moth (Lepidoptera: Lymantriidae) egg mass distribution. *Environmental Entomology* 18: 840-843.

Brennan E.J., J.G. Else & J. Altmann. 1985. Ecology and bahaviour of a pest primate: vervet monkeys in a tourist-lodge habitat. *African Journal of Ecology* 23: 35-44.

Broadbent E.N., Asner G.P., Keller M., Knapp D.E. Oliveira P.J.C. & J.N. Silva. 2008. Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. *Biological Conservation* 141: 1745-1757.

Butynski T.M. 1985. Primates and their conservation in the Impenetrable (Bwindi) Forest, Uganda. *Primate Conservation* 6: 63-72.

Butynski T.M. & J. Kalina. 1998. *Gorilla tourism: A critical look.* In Millner-Gulland E.J. & R. Mace (Eds.) *Conservation of biological resources*. *Blackwells.* Oxford. UK.

Chapman C.A. & C.A. Peres. 2001. Primate conservation in the new millennium: the role of scientists. *Evolutionary Anthropology* 10:16-33.

Chapman C.A., M.L. Speirs, T.R. Gillespie, T. Holland & K.M. Austad. 2006. Life of the edge: Gastrointestinal parasites from the forest edge and interior primate groups. *American Journal of Primatokogy* 68: 397-409.

Chapman C.A. & S.R. Balcomb. 1998. Population characteristics of howlers: Ecological conditions or group history. *International Journal of Primatology* 19: 385-403.

Christie F.J. & D.F. Hochuli. 2009. Responses of wasp communities to urbanization: effects on community resilience and species diversity. *Journal of Insect Conservation* 13: 213-221.

Cordeiro N.J. & H.F. Howe. 2001. Low recruitment of trees dispersed by animals in African forest fragments. *Conservation Biology* 15: 1733-1741.

Crooks K.R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conservation Biology* 16: 488-502.

Curran L.M., I. Caniago, G.D. Paoli, D. Astianti, M. Kusneti, M. Leighton, C.E. Nirarita & H. Haeruman. 1999. Impact of El Niño and Logging on Canopy Tree Recruitment in Borneo. *Science* 286: 2184 - 2188

Davies K.F., C.r. Margules & J.F. Lawrence. 2000. Which traits of species predict population declines in experimental forest fragments? *Ecology* 81: 1450-1461.

Dauber J., M. Hirsch, D. Simmering, R. Waldhardt, A. Otte & V. Wolters. 2003. Landscape structure as an indicators of biodiversity: matrix effects on species richness. *Agriculture, Ecosystems and Environment* 98: 321-329.

de Melo F.P.L.., R. Dirzo & M. Tabarelli. 2006. Biased seed rain in forest edges: Evidence from the Brazilian Atlantic forest. *Biological Conservation* 132: 50-60.

Didham R.K. & J.H. Lawton. 1999. Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. *Biotropica* 31: 17-30.

Didham R.K., P.M. Hammond, J.H. Lawton, P. Eggleton & N.E. Stork. 1998. Beetle species responses to tropical forest fragmentation. *Ecological Monographs* 68: 295-323.

Done T.J. 1987. Simulation of the effects of *Acanthaster planci* on the population structure of massive corals in the genus Parites: evidence of population resilience? *Coral Reefs* 6: 75-90.

Fagan W.F., M.-J. Fortin & C. Soykan. 2003. Integrating edge detection and dynamic modeling in quantitative analyses of ecological boundaries. *BioScience* 53: 730-738.

Fedigan L.M. & K. Jack. 2001. Neotropical primates in a regenerating Costa Rican dry forest: a comparison of howler and capuchin population patterns. *International Journal of Primatology* 22: 109-125.

Fedigan L. & L.M. Fedigan. 1988. *Cercopithecus aethiops: a review of field studies*. In Gautier-Hion A., F. Bourlière & J.-P. Gautier. *A primate radiation: evolutionary biology of the African guenons*. Cambridge University Press. Cambridge. UK. Pp. 389-411.

Fimbel C. 1994. The relative use of abandoned farm clearings and old forest habitats by primates and a forest antelope at Tiwai, Sierra Leone, West Africa. *Biological Conservation* 70: 277-286.

Foggo A., C.M.P. Ozanne, M.R. Speight & C. Hambler. 2001. Edge effects and tropical forest canopy invertebrates. *Plant Ecology* 153: 347-359.

Forman R.T.T. 1995. *Land mosaics: the ecology of landscapes and regions*. Cambridge University Press. New York.

Gascon C., G.B. Williamson & G.A.B. da Fonseca. 2000. Receding forest edges and vanishing reserves. *Science* 288: 1356-1358.

Gascon C., T.E. Lovejoy, R.O. Bierregaard Jr., J.R. Malcolm, P.C. Stouffer, H.L. Vasconcelos, W.F. Laurance, B. Zimmerman, M. Tocher & S. Borges. 1999. Matrix habitat and species richness in tropical forest remnants. *Biological Conservation* 91: 223-229.

Gathua J.M. 2000. *Intraspecific variation in foraging patterns of redtail monkeys (Cercopithecus ascanius) in the Kakamega Forest, Kenya*. Dissertation. Columbia University.

Gautier-Hion A. 1988. *The diet and dietary habits of forest guenons*. In Gautier-Hion A., F. Bourlière, J.-P. Gautier & J. Kingdon (Eds.). *A primate radiation: evolutionary biology of the African guenons*. Cambridge University Press. Cambridge. UK. Pp. 257-283.

Gillepsie T.R. & C.A. Chapman. 2006. Prediction of parasite infection dynamics in primate metapopulations based on attributes of forest fragmentation. *Conservation Biology* 20: 411-448.

Hamberg L., S. Lehvavirta & J. Kotze. 2009. Forest edge structure as a shaping factor of understorey vegetation in urban forest in Finland. *Forest Ecology and Management* 257: 712-722.

Hartshorn G.S. 1989. Application of gap theory to tropical forest management: natural regeneration on strip clear-cuts in the Peruvian Amazon. *Ecology* 70: 567-576.

Harvey C.A. 2000. Windbreaks enhance seed dispersal into agricultural landscapes in Monteverde, Costa Rica. *Ecological Applications* 10: 155-173.

Hooks C.R.R., R.R. Pandey & M.W. Johnson. 2003. Impact of avian and arthropod predation on lepidopteran caterpillar densities and plant productivity in an ephemeral agroecosystem. *Ecological Enthomology* 28: 522-532.

Hope K., M.L. Goldsmith & T. Graczyk. 2004. Parasitic health of olive baboons in Bwindi Impenetrable National Park, Uganda. *Veterinary Parasitology* 122: 165-170.

Illius A.W. & C. Fitzgibbon, 1994. Costs of vigilance in foraging ungulates. *Animal Behavior* 47: 481-484.

Irwin M. 2008. Diademed sifaka (P*ropithecus diadema*) ranging and habitat use in continuous and fragmented forest: Higher density but lower viability in fragments? *Biotropica* 40: 231-240.

Johns A.D. & S.P. Skorupa. 1987. Responses of rain-forest primates to habitat disturbance: a review. *International Journal of Primatology* 8: 157-191.

Kaplin B.A. 2002. *Terrestriality and the maintenance of the disjunct geographical distribution in the lhoesti group*. In Glenn M.E. & M. Cords (Eds.). *The guenons: Diversity and adaptation in African Monkeys*. Kluwer Academic/Plenum Publishers. New York. Pp. 49-60.

Kaplin B.A. & T.C. Moermond. 2000. Foraging of the Mountain Monkey (*Cercopithecus lhoesti*): Implications for its evolutionary history and use of disturbed forest. *American Journal of Primatology* 50: 227-246.

Kapos V., E. Wandelli, J.L. Camargo & G. Ganade. 1997. *Edge-related changes in environmental and plant responses due to forest fragmentation in central Amazonia*. In Laurance W.F., R.O. Bierregaard Jr. (Eds.). *Tropical forest remnants. Ecology, management and conservation of fragmented communities.* University of Chicago Press. Chicago. Pp. 33-44.

Kingdon J. 1997. *The Kingdon field guide to African mammals.* Academic Press San Diego.

Köndgen S., H. Kühl, P.K. N'Goran, P.D. Walsh, S. Schenk, N. Ernst, R. Biek, P. Formenty, K. Mätz-Rensing, B. Schweiger, S. Junglen, H. Ellerbrok, A. Nitsche, T.Briese, W.I. Lipkin, G. Pauli, C. Boesch & F.H. Leendertz. 2008. Pandemic human viruses cause decline of endangered great apes. *Current Biology* 18: 260-264.

Laurance W.F. 2008. Theory meets reality: How habitat fragmentation research has transcended island biogeography theory. *Biological Conservation* 141: 1731-1744.

Laurance S.G.W. 2004. Responses of understory rain forest birds to road edges in central Amazonia. *Ecological Applications* 14: 1344-1357.

Laurance W.F. 2003. Foreword: *Primates as icons for conservation*. In Marsh L.K. (Ed.). *Primates in fragments: Ecology and conservation*. Kluwer Academic/Plenum Publishers. New York. Pp. xi-xii.

Laurance W.F. & E. Yansen. 1991. Predicting the impacts of edge effects in fragmented habitats. *Biological Conservation* 55: 77-92.

Lawes J.M. 2002. *Conservation of fragmented populations of Cercopithecus mitis in South Africa: the role of reintroduction, corridors and metapopulation ecology*. In Glenn M.E. & M. Cords (Eds.). *The guenons: Diversity and adaptation in African Monkeys*. Kluwer Academic/Plenum Publishers. New York. Pp. 375-392.

Lehman S.M., A. Rajaonson & S. Day. 2006. Edge effects and their influence on lemur density and distribution in Southeast Madagascar. *American Journal of Physical Anthropology* 129: 232-241.

Leopold A. 1933. *Game management*. Charles Scribner's Sons. New York.

Lovejoy T.E., R.O. Bierregaard, Jr., A.B. Rylands, J.R. Malcolm, C.E. Quintela, L.H. Harper, K.S. Brown, Jr., A.H. Powell, H.O.R. Schubart & M.B. Hays. 1986. *Edge and other effects of isolation on Amazon forest fragments*. In Soulé M.E. (Ed.). *Conservation biology: The science of scarcity and diversity.* Sinauer Associates, Inc. Sunderland. Massachusetts. Pp. 257-285.

MacArthur R.H. & E.O. Wilson. 1967. *The theory of island biogeography.* Princeton University Press. Princeton.

Major R.E., F.J. Christie & G. Gowing. 2001. Influence of remnant and landscape attributes on Australian woodland bird communities. *Biological Conservation* 102: 47–66

Marsh L.K. 2003. *Primates in fragments: Ecology and conservation*. Kluwer Academic/Plenum Publishers. New York.

Matlack G.R. 1994. Vegetation dynamics of the forest edge-trends in space and successional time. *Journal of Ecology* 82: 113-124.

May E. 1982. Speciation and macroevolution. *Evolution* 36: 1119-1132.

McClanahan T.R. & R.W. Wolfe. 1993. Accelerating forest succession in a fragmented landscape: the role of birds and perches. *Conservation Biology* 7: 279-288.

McIntyre S. & G.W. Barrett. 1992. Habitat variegation, an alternative to fragmentation. *Conservation Biology* 6: 146-147.

McIntyre S. & R. Hobbs. 1999. A framework for conceptualizing human effects on landscapes and its relevance to management and research models. *Conservation Biology* 13: 1282-1292.

McNeilage A., A.J. Plumptre, A. Brock-Doyle & A. Vedder. 2001. Bwindi Impenetrable National Park, Uganda: Gorilla census 1997. *Oryx* 35: 39-47.

Mesquita R.C.G., P. Delamônica & W.F. Laurance. 1999. Effect of surrounding vegetation on edge-related tree mortality in Amazonian forest fragments. *Biological Conservation* 91: 129-134.

Mittermeier R. 1997. Foreword. In Sleeper B. (Ed.). *Primates. The amazing world of lemurs, monkeys and apes.* Chronicle Books. San Francisco. Pp. 6-11.

Mönkkönene M. & P. Reunanen. 1999. On critical thresholds in landscape connectivity: a management perspective. *Oikos* 84: 302-305.

Murcia C. 1995. Edge effect in fragmented forests: Implications for conservation. *Trends in Ecology & Evolution* 10: 58-62.

Naughton-Treves L., Treves, A. Chapman C. & R. Wrangham. 1998. Temporal patterns of crop-raiding by primates: linking food availability in croplands and adjacent forest. *Journal of Applied Ecology* 35: 596-606.

Naughton-Treves L. 1996. *Uneasy neighbours: Wildlife and farmers around Kibale National Park*. Dissertation. University of Florida. Gainesville.

Newman A. 1990. *Tropical rainforest. A world survey of our most valuable and endangered habitat with a blueprint for its survival*. Eddison Sadd Editions. NY.

Newmark W.D. 2001. Tanzanian forest edge microcrimatic gradients: dynamic patterns. *Biotropica* 33: 2-11.

Noss R.F. 1991. Effects of edge and internal patchiness on avian habitat use in an old-growth hammock. *Natural Areas Journal* 11:34-47.

Odum E.P. 1971. *Fundamentals of Ecology.* W.B. Saunders Company. Philadelphia.

Olupot W. 2004. *Boundary edge effects in Bwindi Impenetrable National Park*. Institute of Tropical Forest Conservation. Uganda.

Olupot W. 2009. A variable edge effect on trees of Bwindi Impenetrable National Park, Uganda, and its bearing on measurement parameters. *Biological Conservation* 142: 789-797.

Onderdonk D.A. & C.A. Chapman. 2000. Coping with forest fragmentation: the primates of Kibale National Park, Uganda. *International Journal of Primatology* 21: 587-611.

Owen-Smith N. 1990. Demography of a Large Herbivore, the Greater Kudu (*Tragelaphus strepsiceros*) in Relation to Rainfall. *Journal of Animal Ecology* 59: 893-913.

Paton P.W. 1994. The effect of edge on avian nest success: how strong is evidence? *Conservation Biology* 8: 17-26.

Pimm S.L, H. L. Jones & J. Diamond. 1988. On the risk of extinction. *American Naturalist* 132: 757-785.

Reese K.P. & J.T. Ratti. 1988. *Edge effect: A concept under scrutiny*. Transactions of the North American Wildlife Resources Conference 53rd. Pp. 127-136.

Richard A.F., S.J. Goldstein & R.E. Dewar. 1989. Weed Macaques: The evolutionary implications of Macaques feeding ecology. *International Journal of Primatology* 10: 569-594.

Sanderson E.W., M. Jaiteh, M.A. Levy, K.H. Redford, A.V. Wannebo & G. Woolmer. 2002. The human footprint and the last of the wild. *BioScience* 52: 891-904.

Schwarzkopf L. & A.B. Rylands. 1989. Primate species richness in relation to habitat structure in Amazonian rainforest fragments. *Biological Conservation* 48: 1-12.

Siex K. 2003. *Effects of population compression on the demography, ecology, and behavior of Zanzibar red colobus monkeys (Procolobus kirkii)*. Dissertation. Duke University.

Sisk T.D. & C. Margules. 1993. *Habitat edges and restoration: methods for quantifying edge effects and predicting the results of restoration efforts*. In Saunders D.A. & P.R. Erlich (Eds.). *Nature Conservation 3: reconstruction of fragmented ecosystems.* Surrey Beatty and Sons. Pp. 57-69.

Sisk T.D., N.M. Haddad & R. Ehrlich. 1997. Bird assemblages in patchy woodlands: Modeling the effects of edge and matrix habitats. *Ecological Applications* 7: 1170-1180.

Soulé M.E. & J. Terborgh. 1999. *Continental conservation*. Island Press. Washington D.C.

Stouffer P.C. & R.O.J. Bierregaard. 1995. Use of Amazonian forest fragments by understory insectivorous birds. *Ecology* 76: 2429-2445.

Strauss S.Y. 1991. Indirect effects in community ecology: their definition, study and importance. *Tree* 6: 206-209.

Swihart R.K., T.M. Gehring, M.B. Kolozsvary & T.E. Nupp. 2003. Responses of 'resistant' vertebrates to habitat loss and fragmentation: the importance of niche breadth and range boundaries. *Diversity and distributions* 9: 1-18.

Tashiro Y. 2005. Frequent insectivory by two guenons (*Cercopithecus lhoesti* and *Cercopithecus mitis*) in the Kalinzu Forest, Uganda. *Primates* 47: 170-173.

Terborgh J. 1983. *Five New World Primates: A study in comparative ecology.* Princeton University Press. New Jersey.

Thomas J.W., C. Maser & J.E. Rodiek. 1979. *Edges*. In Thomas J.W. *Wildlife habitats in managed forests – the Blue Mountains of Oregon and Washington.* Agriculture Handbook No. 553. US Department of Agriculture Forest Service. Washington D.C. Pp. 48-59.

Turner I.M. 1996. Species loss in fragments of tropical rain forest: a review of the evidence. *Journal of Applied Ecology* 33: 200-209.

Tutin C.E.G., E.A. Williamson; M.E. Rogers & M. Fernandez. 1991. A case study of a plant-animal relationships: *Cola lizae* and lowland gorillas in the Lopé Reserve, Gabon. *Journal of Tropical Ecology* 7: 181-199.

Twinomugisha D. 2007. *Conservation status and determinants of Golden Monkey (Cercopithecus mitis kandti) abundance in Mgahinga Gorilla National Park.* Dissertation. Makerere University. Uganda.

Ukizintambara T. & C. Thébaud: 2002. *Assessing extinction risks in Cercopithecus Monkeys*. In Glenn M. & M. Cords (Eds.). *The Guenons: Diversity and Adaptation in African Monkeys*. Kluwer Academic/Plenum Publishers. New York. Pp. 393-409.

van der Laan M.J. & M L. Petersen. 2005. Direct Effect Models. *U.C. Berkeley Division of Biostatistics Working Paper Series.* 187. http://www.bepress.com/ucbbiostat/paper187/.

van Schaik C. 2004. *Among orangutans: red apes and the rise of human culture*. Belknap Press of Harvard University Press. Cambridge. Massachusetts.

Vos C.C., J. Verboom, P.E.M. Opdam & C.J.F. Ter Braak. 2001. Toward ecological scaled landscape indices. *American Naturalist* 157: 24-41.

Weiner J. 1995. On the practice of ecology. *Journal of Ecology* 83: 153-1158.

Whittaker R.J. 1998. *Island biogeography: Ecology, evolution, and conservation*. Oxford University Press. Oxford.

Wilcove D.S., C.H. McLellan & A.P. Dobson. 1986. *Habitat fragmentation in the temperate zone*. In Soulé M.E. (Ed.) *Conservation Biology. The Science of Scarcity and Diversity*. Sinauer Associates, Inc. Sunderland. Massachusetts.

Williams-Linera G. 1990. Origin and early development of forest edge vegetation in Panama. *Biotropica* 22: 235-241.

Wilson R.F., M.W. Goosem & G.W. Wilson. 2008. Resilience of arboreal folivores to habitat damage by a severe tropical cyclone. *Austral Ecology* 33: 573-579.

Wolff J.O., E.M. Edge & W.D. Schauber. 1997. Effect of habitat loss and fragmentation on behavior and demography of Gray-tailed voles. *Conservation Biology* 11: 945-956.

Woodroffe R. & J.R. Ginsberg. 1998. Edge effects and extinction of populations inside protected areas. *Science* 280: 2126-2128.

Yahner R.H. 1988. Changes in wildlife communities near edges. *Conservation Biology* 2: 333-339.

Yahner R.H. & C.G. Mahan. 1997. Behavioral considerations in fragmented landscapes. *Conservation Biology* 11: 569-570.

CHAPTER 2

EDGE EFFECTS ON PLANT SPECIES RICHNESS AND HABITAT STRUCTURE IN AN AFROMONTANE FOREST 16 YEARS AFTER INTENSIVE LOGGING

ABSTRACT

Recently, much attention has been given to understanding how deforestation increases the forest edge/interior ratio, how it affects the quality of forest habitats, and how it influences the survival of species. I conducted a study to assess how the distribution of tree, shrub, and understory plant species and habitat structure was influenced by proximity to forest edge in Bwindi Impenetrable National Park, Uganda. Bwindi is a tropical montane forest that was subject to intensive logging at the periphery and selective logging in the interior before 1991, and thereafter occasional illegal tree cutting for firewood and construction has continued. Along the edge of the study site lays a matrix characterized by a mixture of pasturelands and abandoned farmlands. I found that edge effects were less evident along the 15 m, 165 m, 315 m, 1000 m and 1700 m edge-interior gradient but more apparent when the edge zone (< 400 m) was compared with the interior forest zone (> 400 m). Based on these findings I estimated depth of edge effects to penetrate to approximately 400 m from the forest boundary. The edge forest (< 400 m) had relatively more species and a more homogeneous canopy structure than the interior forest (> 400m). Percentage canopy cover, density of pioneer species, density of ferns, vines and herbs were higher at the edge than in the interior of the park. Woodcutting was widespread throughout the study area. Therefore, more conservation efforts are needed to reduce anthropogenic disturbances, and to allow the establishment of softer edges that will buffer negative edge effects and prevent them from penetrating further inside the Bwindi Impenetrable forest.

Key words: Edge effects, anthropogenic disturbances, plant species composition, habitat characteristics, Bwindi Impenetrable National Park, Uganda.

INTRODUCTION

Understanding the range of factors that have historically shaped and continue to affect forest landscapes is of tremendous importance to the conservation of biodiversity (Sanderson, 2002). Deforestation and habitat fragmentation are the dominant factors shaping forested landscapes by creating forest edges, which are one of the most apparent features in disturbed landscapes (Newmark, 2001; Olupot, 2009). These forest edges are generally exposed to high wind velocity, elevated air and soil temperature, and increased light intensity from surrounding agricultural or non-forest matrices. These microclimatic gradients independently or in combination with biotic factors influence the distribution and abundance of plant and animal species from the edge towards the forest interior (Newmark, 2001; Tabarelli et al., 2008).

Several studies have compared the distribution, regeneration, re-colonization, and survival of species among fallow matrices, forest edges, and interior forest in relation to climatic factors (Stamps et al., 1987; Williams-Linera, 1990a; Andrén, 1995). Stamps et al. (1987) found that higher temperatures at forest edges can significantly alter plant species composition and increase tree mortality. The resulting gaps and clearings expose understory vegetation to desiccation (Chen et al., 1992) and at the same time provide favorable conditions for pioneer species to thrive (Tabarelli et al., 2008).

Plant and animal species respond differently to varying intensity and depth of edge conditions that shape edge and interior forest habitats (Williams-Linera, 1990b; Olupot, 2009). For example, Lehman et al. (2006) identified edge-tolerant, edge-intolerant, and omnipresent lemur species in Madagascar.

In this study, I investigated edge effects on the distribution and composition of canopy and understory tree and terrestrial herb species, and on the structure of different habitats in the tropical montane forest of Bwindi Impenetrable National Park, Uganda. Specifically, I tested the impact of edge effects and assessed the legacy of past intensive logging activities on the distribution and abundance of tree and terrestrial herb species as well as how current disturbances alter the characteristics of edge microhabitats in the Bwindi impenetrable forest.

METHODS

Study area

Bwindi Impenetrable National Park, hereafter Bwindi, covers 321 km^2 astride the districts of Kabale, Kisoro and Rukungiri in southwestern Uganda (between latitudes 0°53' and 1°08'S and longitudes 29°35' to 29°50'E, Figure 1). Bwindi is characterized by steep slopes ranging from 1190 m to 2607 m above sea level (a.s.l.). The vegetation is generally influenced by elevation, aspect, soil, and disturbance (Ganas et al., 2004; Olupot, 2004; Ganas et al., 2009). Due to relatively high acidity and erosion, tree regeneration and productivity are very low on most steep hillsides (Butynski, 1984; Howard, 1991).

Bwindi became a national park in 1991. Prior to this, although mechanized commercial logging had never occurred in Bwindi due to its extremely rugged terrain, pit saw logging was extensive (Butynski & Kalina, 1993; Pomeroy, 1990). Logging has created large gaps and clearings that are maintained by elephant activities in some parts of the forest (Babaasa, 2000). These clearings are dominated by pioneer species such as

Neoboutonia macrocalyx, Alchornea hirtella, Macaranga kilimandscharia and *Polyscias fulva.* Bwindi's name, "impenetrable", derives from the dense layer of herbs, shrubs, and lianas such as *Mimulopsis* spp., *Rubus* spp.*, Psychotria* spp. and *Smilex* spp, that colonize open slopes and valleys. Primary forest species such as *Chrysophyllum albidium* are relatively common on slightly logged and unlogged ridge tops in association with *Strombosia scheffleri, Podocarpus milanjianus,* and *Olea capensis*. Bwindi has more than 200 tree species, 47% of the country's total, with 10 endemic species, 16 tree species restricted to southwest Uganda, and one (*Lovoa swynertonii* – Meliaceae) internationally threatened species (Howard, 1991; UNEP-WCMC, 2003).

Despite the impact of past logging (Figure 1), Bwindi remains one of the few large expanses of forest in East Africa where lowland and montane vegetation communities meet. The park is characterized by high endemism, which has been attributed to its location in the Albertine Rift Montane refugium (Hamilton, 1984). This situation has led to extremely high biodiversity, and there is evidence that Bwindi is one of the most diverse forests in East Africa in terms of tree species (UNEP-WCMC, 2003). Bwindi was designated as a world heritage site in 1994 and classified as one of the 29 most important forests for conserving plant diversity in Africa (UNEP-WCMC, 2003). Bwindi is therefore one of the most important areas for species conservation in Uganda.

My study site encompassed four small watersheds characterized by ravines and mountains ranging from 1900 m to 2400 m a.s.l. In forest adjacent to the matrix of pasture and farmlands on the eastern side there was a "multiple use zone" established near the edge for local beekeepers. Several large forest clearings were found throughout the site, mostly towards the interior forest (Bitariho et al., 2006; Babaasa et al., 2004).

The matrix outside the park directly adjacent to my study site was characterized from the south towards the northeast by pasturelands where cattle grazed regularly, a marsh containing a small stream, an abandoned farm with sparsely distributed remnant indigenous forest trees and shrubs including *Bridelia micrantha*, *Psychotria* spp., *Myrianthus holstii* and *Rhys natalensis*, and an abandoned farmland with sparsely distributed Australian black wattle (*Acacia mearnsii*).

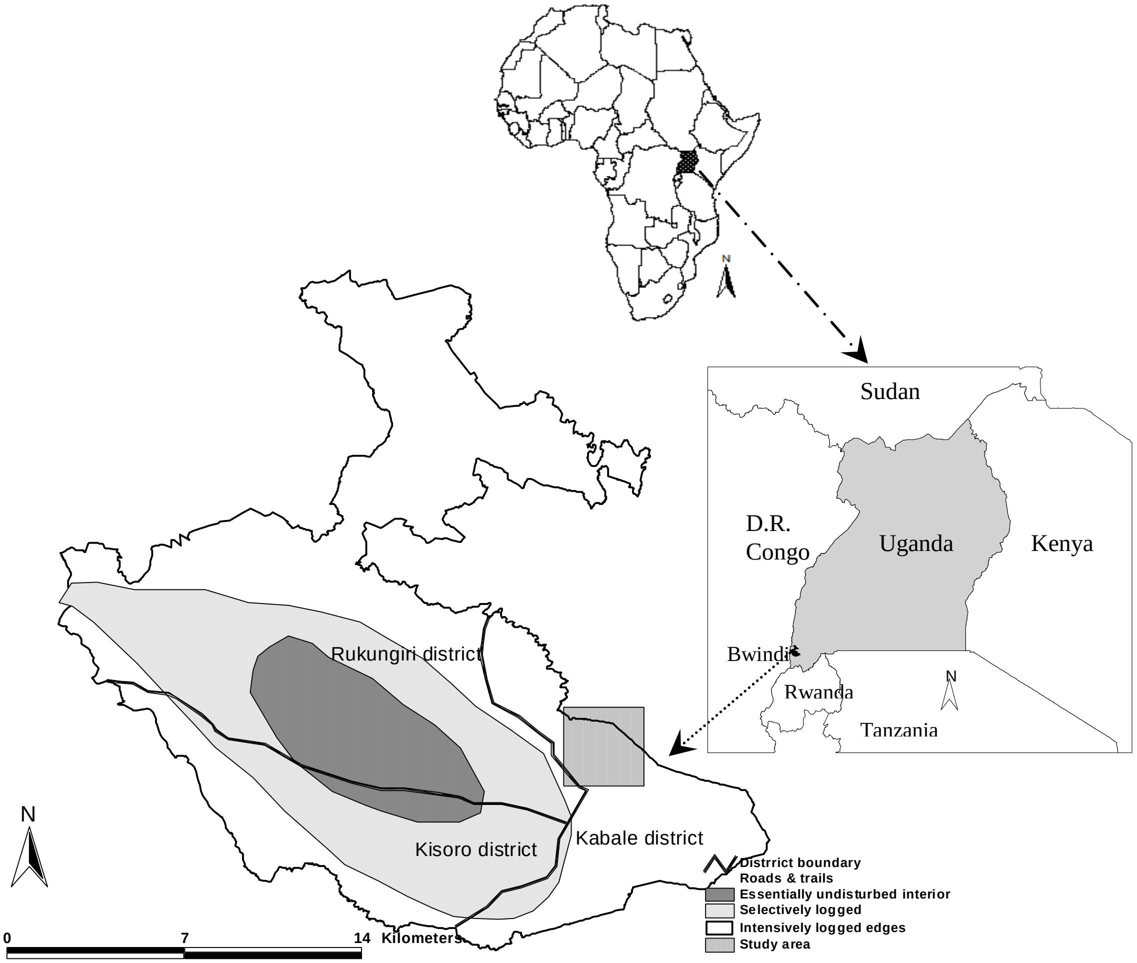

Figure 1. Bwindi Impenetrable National Park in Uganda. The extent of logging intensity was adapted from Howard (1991).

Vegetation sampling

I sampled vegetation following an edge to interior at 15 m, 165 m, 315 m, 1000 m and 1700 m. Ten circular plots (10 m radius) were systematically placed at each distance 100 m at least from one another (Figure 2).

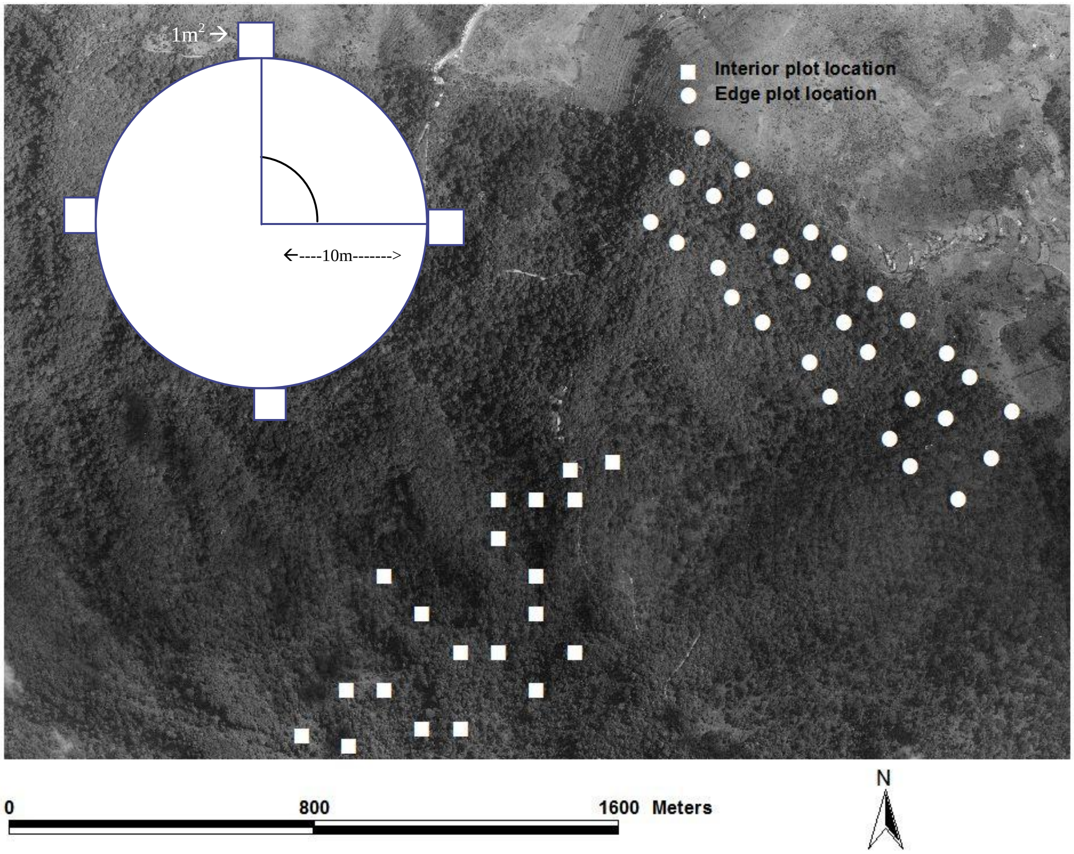

Figure 2. Location of vegetation plots and quadrats at the study site in Bwindi Impenetrable National Park, Uganda. The edge and interior vegetation plots are represented by white circles and squares respectively, while the big white circle is an enlargement of a plot to illustrate the configuration of the four quadrats (white squares) at each right angle.

All plots were geo-referenced in UTM ARC 1960 using Garmin 12XL. Accuracy was improved by a GPS antenna in dense canopy forest locations. Within each edge and interior plot, (1) all tree stems ≥5 cm of diameter at breast height (DBH) were identified to species when possible and (2) the DBH and height of each tree stem was measured.

I established four 1 m^2 quadrats at right angles from the central axis of each plot to sample understory plants including seedlings and terrestrial herbaceous vegetation (THV; n = 200 quadrats; Figure 2). On each quadrat, I (1) estimated percent cover of THV using a 10 cm x 10 cm frame (Brower et al., 1997), (2) measured the canopy vegetation cover from the center using a densiometer (Lemmon, 1957) and (3) counted all shrub, sapling and herb stems, and clumps of ferns. All climbers and herbs coming from outside the quadrats were excluded from the analysis. On the ten vegetation plots established along the 15 m transect from the edge, I subsampled edge habitat and pooled together data from the ten quadrats located at 5 m from forest edge, twenty quadrats at 15 m, and ten at 25 m (Figure 3).

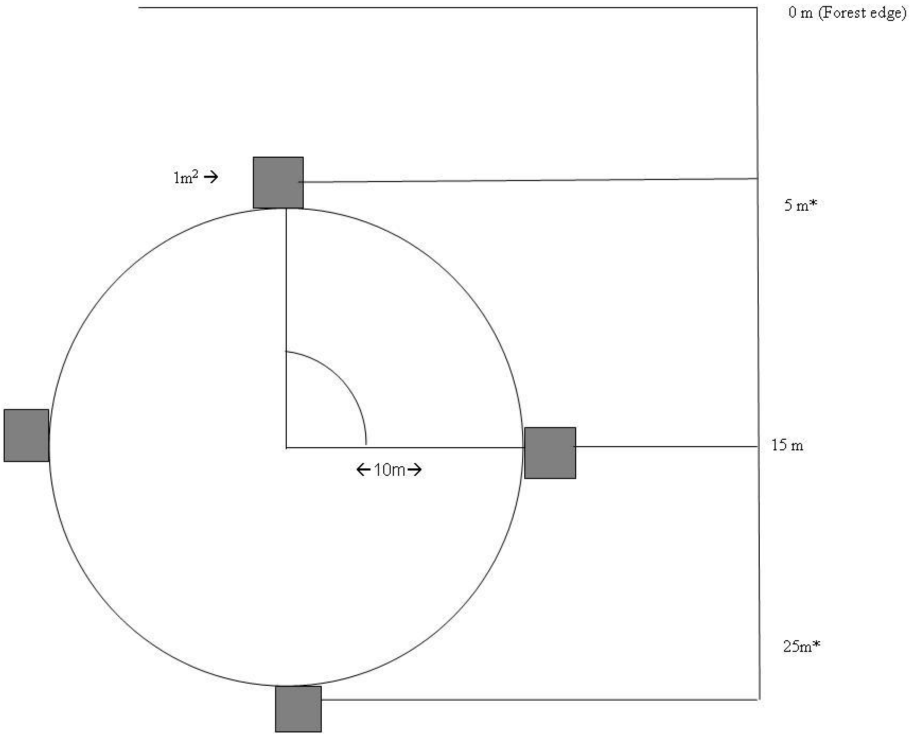

Figure 3. Illustration of the localization of quadrats for sampling understory species (*Quadrats located at and between 5 m and 25 m from the forest edge).

I identified all tree, shrub and saplings in the plots, and all seedlings and understory herb species in the quadrats when possible, and took samples of unknown species to the Institute of Tropical Forest Conservation (ITFC) herbarium for identification. I also documented signs of illegal wood cutting and trees bent by wind or damaged by large animals, such as gorillas and elephants, or other disturbances.

Data analysis

I assessed similarities or differences between the edge and interior forest habitats by comparing density, dominance, and mean height of tree species, the density of understory vegetation, and percent of canopy tree cover and THV cover across the five distance zones: 15 m, 165 m, 315 m, 1000 m and 1700 m. According to trends in the results, I established the depth of edge effects at 400 m and compared variables between the edge (0 m to 400 m) and the interior (400 m to 2200 m) habitats on the pooled data from each area. Forest habitat types in Bwindi have been described relative to their canopy openness or ground vegetation cover (Nkurunungi et al., 2004; Ganas et al., 2004; Ganas et al., 2009). I also referred to percentage of canopy and ground vegetation cover to characterize and make a distinction between the edge and interior habitats.

I calculated the dominance index of each tree species by adding together relative frequency, relative density, and relative cover (basal area) for each species (Brower et al., 1997). I also calculated the Simpson's diversity index $D=1-\Sigma\ [pi^2]$, where pi is a proportional cover of the i^{th} species in a plot. D ranges between 0 and 1, with 1 showing greater sample diversity. D is the probability that two randomly chosen individuals from a sample will belong to different species or different category. It takes into account both richness and evenness. D is also called a dominance index, weighting towards the abundance of the most common species (Krebs, 1989); according to Lande (1996), D is an unbiased estimator of diversity.

I computed vegetation composition comparisons at different distances and scales: among 15 m, 165 m, 315 m, 1000 m and 1700 m, and between combined edge (< 400 m) and interior (> 400 m) zones. Analysis of variance (ANOVA) was used to compare tree and understory species density, dominance and diversity, tree species height, vegetation canopy and ground cover, distribution in pole and firewood cutting across the five zones. To meet the assumptions of normality, the analysis was run on the square-root of tree species densities per ha. ANOVA was also used to compare the density distribution of understory edge species at a small scale: 5 m, 15 m and 25 m from the edge, and tree density and vegetation canopy cover between the edge forest (< 400 m) and the interior forest (> 400 m). The Friedman two-way analysis of variance by ranks was used to compare the density of fern species and the abundance of vines and terrestrial herbs across the five zones. The Friedman test was also used to analyze the density and dominance of primary and pioneer tree species between the edge (< 400 m) and the interior (> 400 m) forests. The Friedman test is a non-parametric test similar to the parametric repeated measures ANOVA. The test statistic for the Friedman test is a Chi-square (χ^2) with (a-1) degrees of freedom, where ‘a’ is the number of repeated measures. I used SPSS 16.0 for Windows in all statistical analyses.

RESULTS

Vegetation composition and habitat characteristics across five zones

I identified 74 families comprising 52 tree and shrub species, 57 terrestrial herb species, 16 shrub species, 13 vine species and 4 fern species, including four unidentified terrestrial herb species and one unidentified Rubiaceae shrub species tallying to 143 species (Appendix 1 & 2). The most common species were pioneer species such as *Xymolos monospora*, *Neoboutonia macrocalyx*, *Galiniera coffeioides*, *Macaranga kilimandscharica*, *Nuxia congesta*, *Psychotria mahonii*, *Rhys natalensis*, *Dombeya goetzenii*, *Allophyllum abyssinic*a and *Syzygium guineense* was the most abundant primary forest tree species.

There was no significant difference in tree species dominance across the five zones from edge to interior (ANOVA: $F_{4, 173}$=0.636, p=0.637, Figure 4 and Table 1).

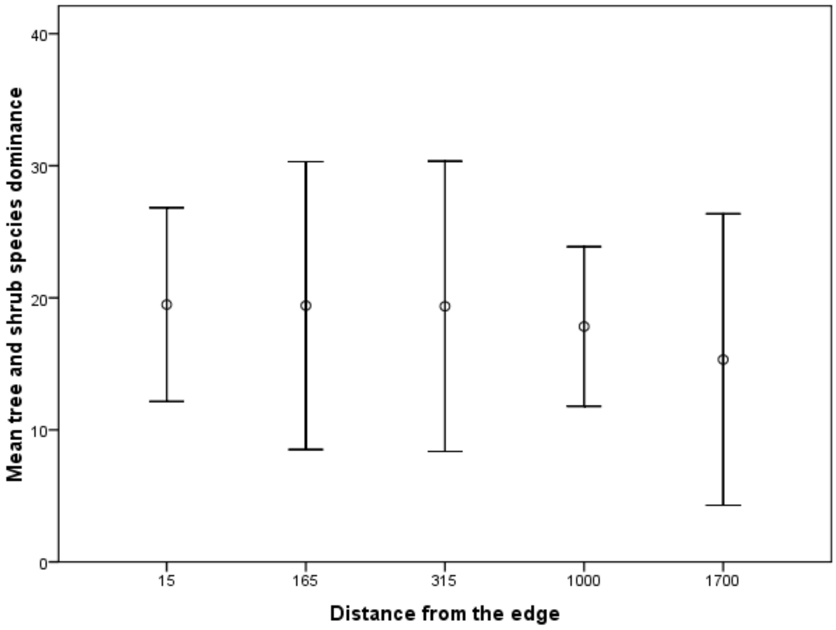

Figure 4. Mean and standard deviation of tree and shrub dominance indices. There was no difference in species dominance index across zones. The minimum and maximum species dominance values ranged from 0.012 to 73.42; 0.002 to 201.16; 0.003 to 188.44; 3.20 to 63.91 and 3.2 to 137.61 for zone 15 m, 165 m, 315 m, 1000 m and 1700 m, respectively.

Table 1. Dominance index of 18 most dominant species of trees and shrubs in the study area in Bwindi Impenetrable National Park. The index value for the three most dominant species is highlighted in gray in each zone.

Tree species	**15 m**	**165 m**	**315 m**	**1000 m**	**1700 m**
Xymolos monospora	70.29	201.16	188.44	63.91	9.61
Neoboutonia macrocalyx	19.20			44.74	137.61
Galiniera coffeoides	73.48	95.79	19.18	9.59	3.20
Macaranga kilimandscharia	41.55	28.74	51.11	35.15	16.02
Nuxia congesta	70.31	15.98	25.63	19.21	9.67
Psychotria mahonii	19.17	31.93		60.72	19.21
Rhys natalensis	47.93	19.17	63.88		
Dombeya goetzenii	3.26	12.79	31.95	41.57	28.82
Allophyllum abyssinica	3.20	41.53	25.55	44.73	
Syzygium guineense	31.96	12.77	60.69	3.20	
Bridelia micrantha	19.17	60.68	25.56		
Maesa lanceolata	22.37	9.63	35.16	19.24	9.63
Polyscias fulva	19.19	38.35	16.03	9.67	
Podocarpus milanjianus	35.14			31.96	3.20
Agauria salicifolia	22.49	3.25	32.07	9.70	
Alchornea hirtella		38.32	12.79	16.06	
Faurea saligna	19.29	6.70	13.04	16.06	9.78
Rytiginia ruwenzoriansis		3.19	12.78	31.95	12.81

There was no significant difference in densities of primary tree species across the edge-interior gradient ($F_{4, 84} = 1.299$, $p = 0.278$); however, the density of pioneer species was significantly different among zones ($F_{4, 234} = 3.329$, $p = 0.011$). The posthoc test showed that zone 1700 m had overall higher density but the lowest dominance of pioneer tree species (Appendix 1).

I found that the distribution of tree and shrub species density and their mean height differed significantly across zones ($F_{4, 49}=3.32$, $p=0.02$ and $F_{4, 49}=2.65$, $p=0.04$, Figures 5 and 6 respectively). A post hoc test showed that zone 1700 m had the lowest tree density compared with zone 165 m and zone 315 m ($p = 0.02$ and 0.001 respectively) while zone 1000 m had on average taller trees than zones 315 m and 1700 m (p=0.007 and 0.013, respectively). *Syzygium guineense* and *Agauria salicifolia* were among the most dominant and tallest tree species in zone 1000 m (Figure 6).

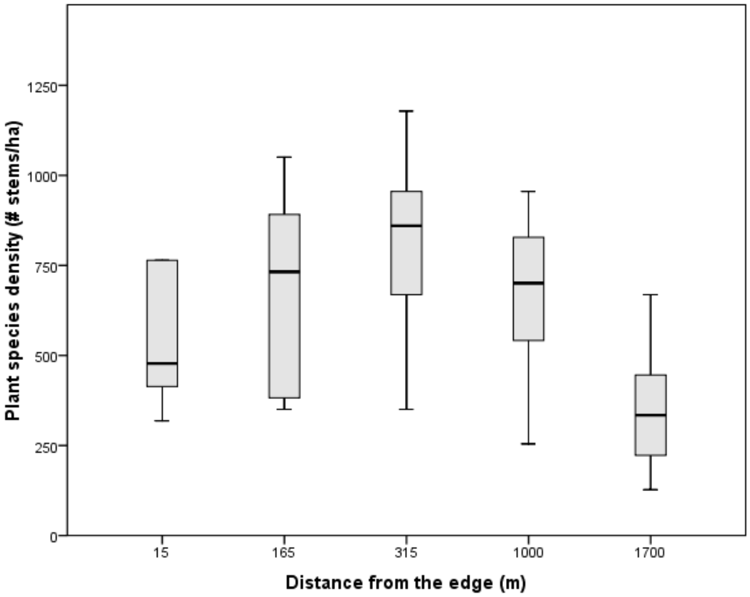

Figure 5: Tree, shrub and flowering plant species density at different distances from forest edge. All stems > 5 cm DBH (Mean = 629.94 ± 293.81 stems/ha, range from 63.69 to 1337.58).

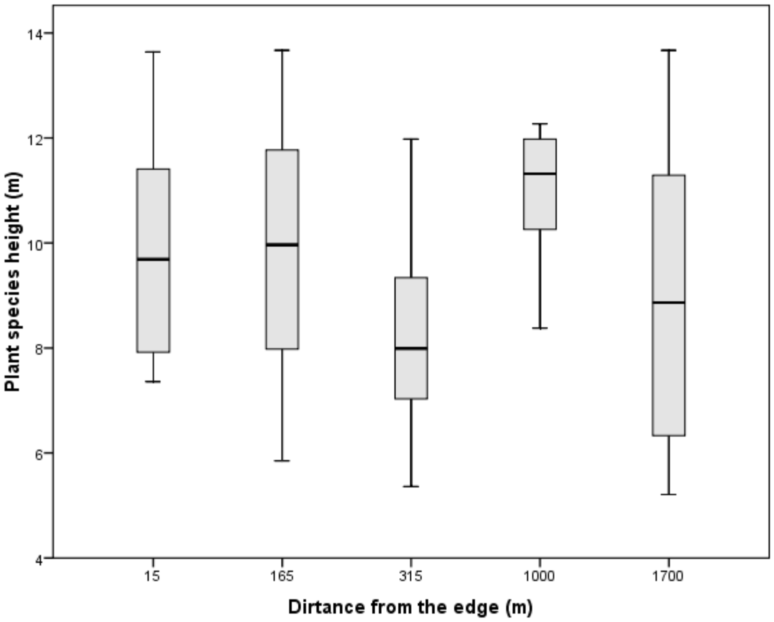

Figure 6. Tree, shrub and flowering plant species height per distance from the forest edge of Bwindi. (Mean = 9.49 ± 2.33 m ranging from 0.1 m for a bent down tree to 32 m).

There was no significant difference in the Simpson diversity index among each of the five zones for tree and large flowering plant species ($F_{1;\,9} = 1.11$, $p = 0.323$). The Simpson diversity index was 0.941 ± 0.005, n = 32; 0.904 ± 0.012, n = 41; 0.901 ± 0.013, n = 35; 0.949 ± 0.004, n = 35 and 0.851 ± 0.024, n = 27 for zones 15 m, 165 m, 315 m, 1000 m and 1700 m respectively.

Canopy cover was significantly different between zones ($F_{4,\,47} = 3.437$, $p = 0.016$). A posthoc test showed that zone 1700 m had a more open canopy than all edge zones, i.e. zones 15 m, 165 m and 315 m ($p < 0.03$), but no difference with zone 1000 m ($p = 0.139$).

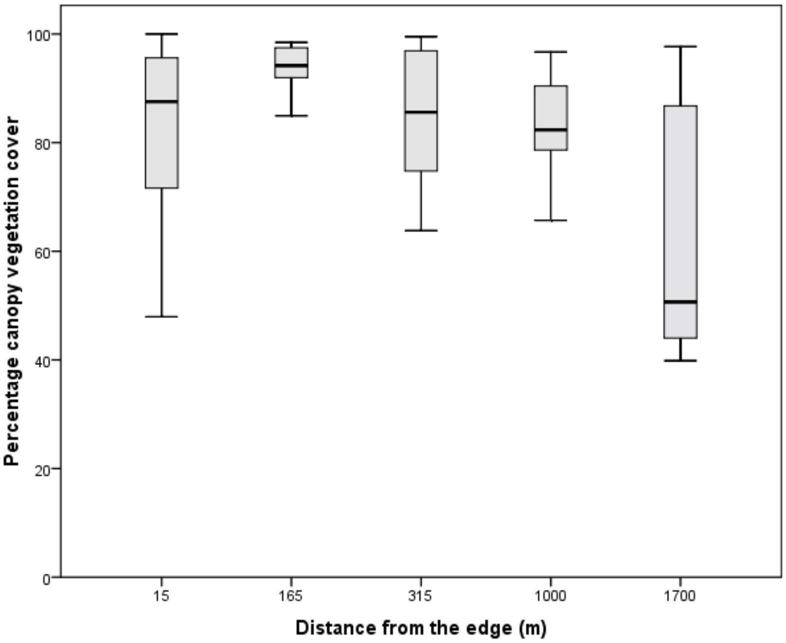

Figure 7. Canopy cover (mean = 80 ± 20 (7-100%), n=48) at different distances from the forest edge of Bwindi.

There was no difference in the density of understory plant species (seedling and herbs that are less than 1 m in height) with distance from edge ($F=_{4, 49} = 1.278$, $p = 0.293$). However, a posthoc analysis showed that understory plant density in zone 15 m (forest edge) was significantly higher than 315 m, zone ($p = 0.043$), but relatively similar to other zones ($p \geq 0.05$) (Figure 8). Zone 15 was dominated by terrestrial herb and fern species including *Drymaria, Commelina, Asplenium, Crassocephalum,* and *Panicum*. Along the 15 m edge transect, there was no difference in the density of understory plant species sampled in the quadrats at 5, 15 and 25 m from the edge ($F_{2; 39} = 0.01$, $p = 0.99$).

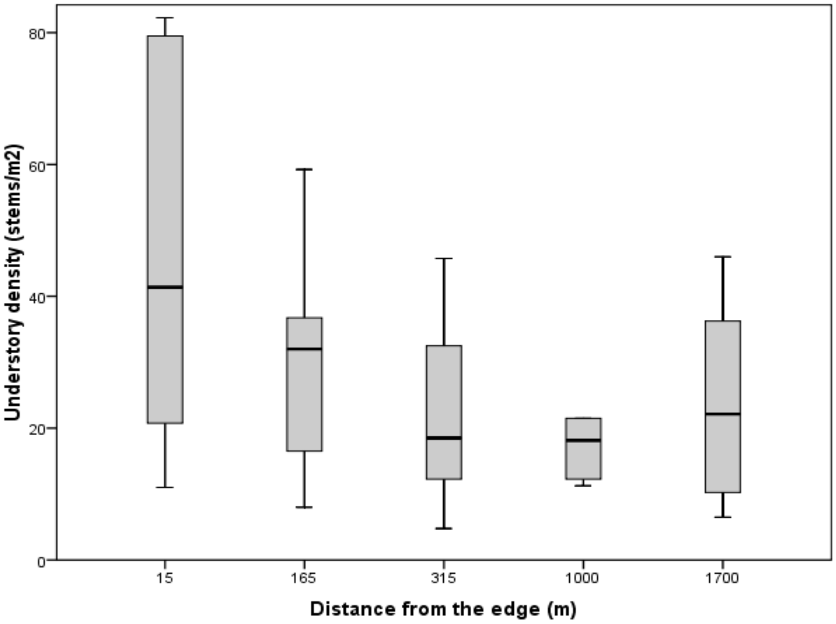

Figure 8. Understory plant species density at the different distances sampled from the forest edge of Bwindi (mean = 31.71 ± 26.27 ranging from 4.75 to 141.75 plants per m^{-2}).

There was no difference in species diversity between understory species across the five zones. The Simpson diversity indices were 0.619 ± 0.013, n = 67; 0.859 ± 0.006, n = 58; 0.823 ± 0.012, n = 55; 0.818 ± 0.010, n = 55 and 0.912 ± 0.005, n = 58 respectively for zone 15 m, 165 m, 315 m, 1000 m and 1700 m.

There was no significant difference in ground vegetation cover among zones ($F_{4, 49} = 0.542$, $p = 0.706$). The ground was mostly covered by *Mimulopsis solmsii*, *Panicun* spp., and ferns at all zones. There was no significant difference in the density of fern species among zones ($\chi^2 = 4.107$, df = 4, $p > 0.05$). There were certain species that did differ with distance from edge: *Asplenium* sp. and *Pteris* sp. were more abundant on the edge, while *Pteridium* sp. and *Cyathea maniana* were more common in the interior (Appendix 2).

Depth of edge effects in the Bwindi Impenetrable forest

I detected a non-monotonic distribution of variables from the edge towards the interior forest. Peaks and troughs were apparent at zones 165 m and 315 m. The density of herbs (m^{-2}) decreased from the edge up to 315 m and increased towards the interior (Friedman $\chi^2_{4;\,57} = 15.75$, $p = 0.003$) (Table 2). The density of vines (m^{-2}) decreased from the edge up to 165 m and then increased towards the forest interior (Friedman $\chi^2_{4;\,12} = 10.02$, $p \leq 0.04$) (Table 2). The density of tree and shrub species and percentage canopy cover were lower at zones 1700 m and 1000 m compared with zones 315 m and 165 m ($F_{4,\,49}=3.32$, $p=0.02$ Figure 5 and $F_{4;\,47} = 3.437$, $p = 0.016$, Figure 7, respectively).

Table 2. Mean density and standard deviation of terrestrial herb and vine species with distance sampled from the forest edge of Bwindi.

Distance zones sampled from forest edge (m)	Mean density of herb species (m^{-2})	Mean density of vine species (m^{-2})
15 m	2.74 ± 14.96	0.73 ± 0.79
165 m	0.94 ± 3.88	0.53 ± 1.06
315 m	0.53 ± 1.46	0.59 ± 0.75
1000 m	0.96 ± 4.82	1.64 ± 4.08
1700 m	0.94 ± 2.59	1.77 ± 4.19

Although not statistically significant, the overall density of understory plant species and the Simpson diversity indices for trees and shrubs decreased from the edge up to 315 m, and then increased towards the interior forest.

Based on these results, I estimated the penetration of edge effects at 400 m inside the forest. Therefore, I grouped together sampling zones 15 m, 165 m and 315 m in the edge forest (< 400 m), while the interior forest (< 400 m) comprised sample plots in zones 1000 m and 1700 m respectively.

Plant species composition, habitat characteristics and anthropogenic disturbances between the edge forest (< 400 m) and interior forest (> 400 m)

The mean percentage (± standard deviation) canopy vegetation cover was significantly higher (87% ± 13) on the edge forest (< 400 m) than in the interior forest (70% ± 25) (> 400 m) ($F_{1, 46} = 9.314$, $p = 0.004$, Figure 7). Species area curves showed that the edge forest had higher species richness than the interior forest (Figure 9). Additionally, the interior forest was characterized by abrupt variation in species composition between plots, therefore more heterogeneous in habitat structure than the edge forest.

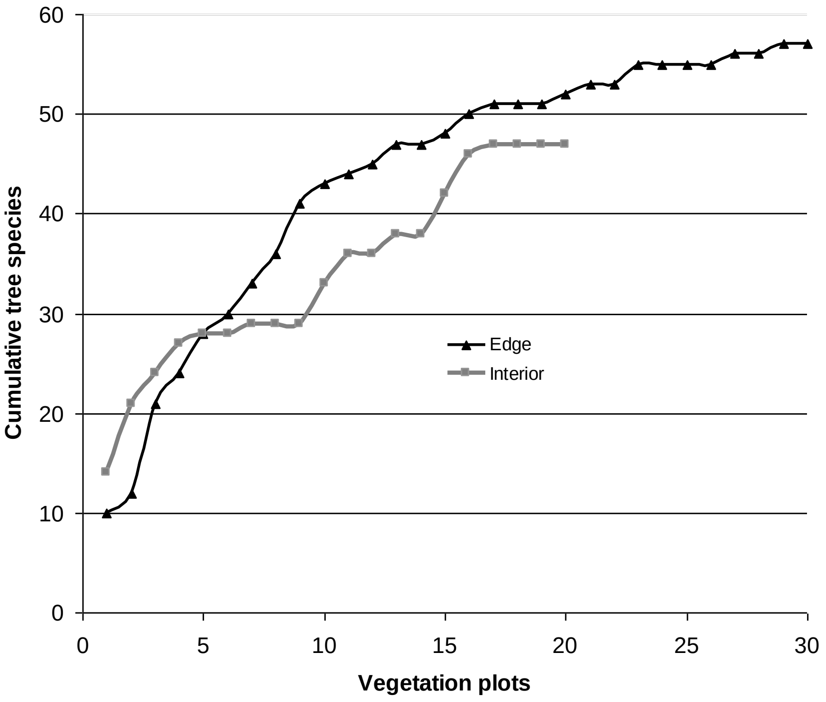

Figure 9. Species area curves for edge and interior forest plots in Bwindi.

The forest edge plots (< 400 m) on average had higher tree and shrub species diversity but lower understory diversity than the interior zone (> 400 m). The diversity index of trees and shrubs was 0.915 and 0.9, while the diversity index of understory plant species was 0.767 and 0.865 respectively for the edge and interior forest. Between the edge and the interior forest there was no significant difference in the dominance of primary tree species (Friedman $\chi^2 = 1.143$, n = 14, p = 0.285). The Friedman ranks were 1.36 and 1.64 respectively. However, the mean dominance of pioneer tree species was higher on the edge than in the interior (Friedman $\chi^2 = 8.000$, N = 50, p = 0.005), with Friedman ranks of 1.70 and 1.30 respectively. In addition, the canopy vegetation of the edge (< 400 m) was more covered that that of the interior (> 400 m) ($F_{1, 47} = 9.314$, p = 0.004) (Figure 10).

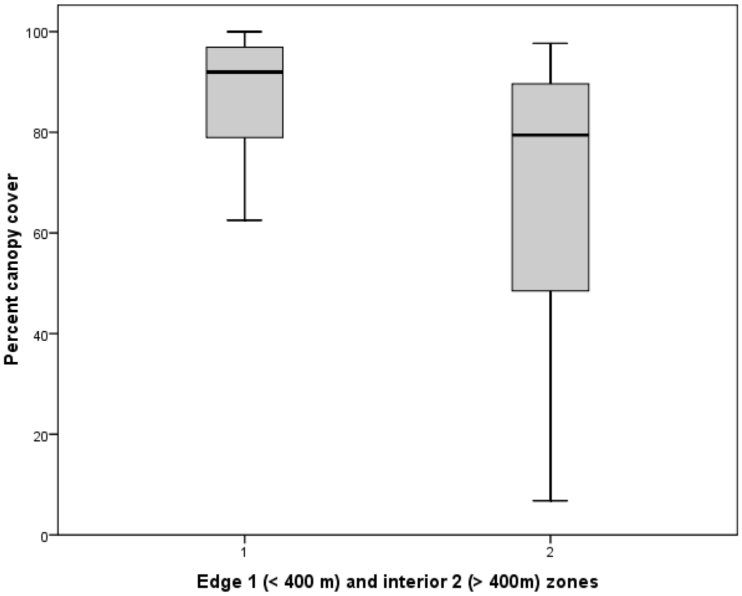

Figure 10. The percent canopy vegetation cover at the forest edge (< 400 m) and interior (> 400 m) forest in Bwindi.

The average percentage of illegal pole and firewood cutting in the edge forest (19 ± 11, range 6 to 38%) was relatively similar to that in the interior (20 ± 12, range 11 to 44%) (> 400 m) (Mann - Whitney z = - 0.315, n = 50, and p = 0.752) (Figure 11).

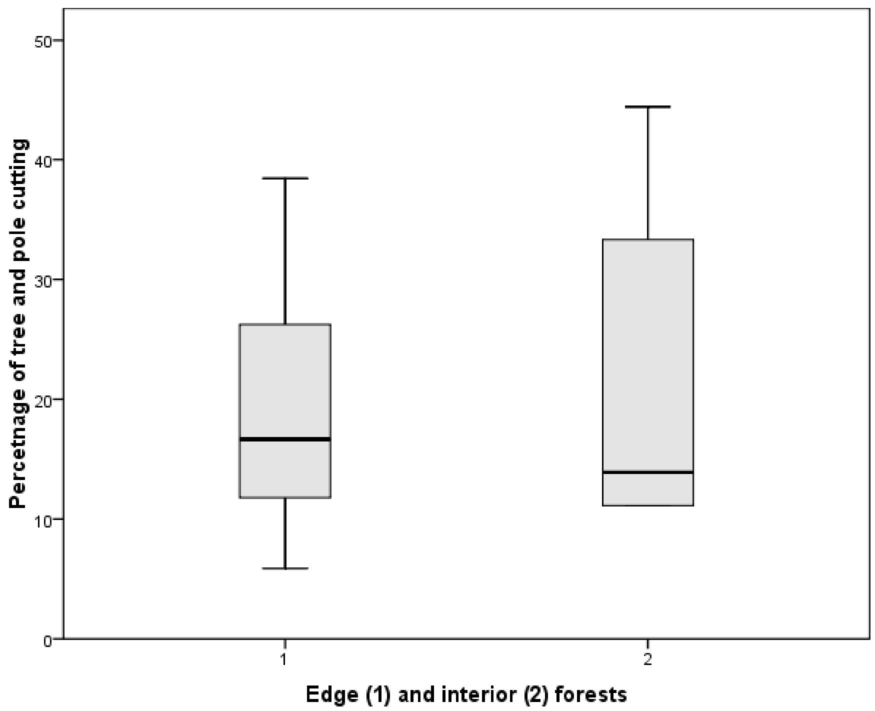

Figure 11. Illegal tree and pole cutting between edge and interior of the Bwindi Impenetrable forest.

DISCUSSION

Vegetation composition and habitat characteristics across the five zones

One of the most challenging aspects of ecological sciences is to identify the mechanisms that explain species distribution and habitat characteristics (Rees et al., 1996). The comparisons of forest edge versus forest interior in this study allowed me to examine two areas with were relatively different in their reactions to edge effects. The forest edge zone (around 15 m) had higher understory plant species density than other more interior zones, likely due to increased light from outside the park. The interior forest (e.g. zone 1700 m) was characterized by large clearings. However, the 1700 m zones had also lower density of understory species and a predominance of ferns, *Rubus* sp. and *Mimulopsis solmsii,* whose clumps can cover a large area of a clearing (Babaasa et al., 2004). The pioneer species had higher dominance indices than primary forest species in the forest edge than interior zones. Similarly, I found an edge to interior decreasing trend in understory species composition. However, as Duncan & Chapman (2003) found in Kibale forest, vine species tended to increase towards the interior of Bwindi forest as opposed to the findings of Fritz & Merriam (1996) and Laurance et al. (2001a).

Besides edge effects, factors such as human activities, presence of exotic species, and land-use history could be additional explanation to differences noted in vegetation structure and composition. Intensive logging can create large open canopies and suitable conditions for pioneer species to penetrate the interior and proliferate (Tabarelli et al., 2008), which appears to be the case in Bwindi, where primary forest species were selectively logged throughout the study area. The Bwindi forest was intensively logged up to approximately 6 km from the edge, an area that Butynski (1984) classified as secondary forest. Consequently, my whole study area consisted of a secondary forest where all logging activities, cessation of logging, and forest regeneration have occurred simultaneously. Therefore, examining edge effects based on the distribution of large trees in a logged forest could provide flawed results.

In such places where human activities have been intense, forest edge effects could be effectively verified by looking at the distribution of understory species. According to Matlack (1993), forest edges tend to show high densities of saplings and shrubs. Schmidt (2005) discussed how plants of the understory flora are the most suitable indicators for site conditions, environmental changes, human impact, and forest dynamics. Understory flora could also be suitable for studying forest edge effects. However, few edge effect studies have been conducted on understory species in tropical forests (Duncan & Chapman, 2003). Testing edge effects from the distribution of the terrestrial herbaceous layer was the first attempt in the Bwindi forest.

Depth of edge effects and characteristics of edge versus interior forest in Bwindi

The distribution of canopy cover, density of pioneer tree species and density of understory plant species were significantly different among study zones and the depth to which these edge-related variables could either be measured at 165m or at 315m from the forest edge, depending on which variables were measured. Such peaks and troughs in patterns of how plant species and habitat structure were influenced by forest edges were explained by Rodrigues (1998) as a result of non-monotonic distribution of edge effects. The non-monotonic pattern was a result of either wind disturbance or niche partitioning and asymmetrical competition that alternate in oppressed and non-oppressed areas

(Rodrigues, 1998). Studies have described multiple depths of edge effects as having additive, opposing, or synergetic influences with peaks and depressions (Ries et al., 2004; Ewers & Didham; 2007; Bossart & Opuni-Frimpong, 2009). Some authors have identified these patterns as neutral edge effects (e.g. Lehman et al., 2006).

In many studies, rather than being at two or more separate distances, the depths of edge effects have been reported at a single distance ranging from a few meters to a few kilometers. When Broadbent et al. (2008) reviewed the literature on edge effects, they found that over 54% had documented edge effects penetrating between 100m and 2km. Olupot and Chapman (2006) and Ewers and Didham (2008) reported edge effects above 250m to 1km. However, it is impossible to measure the depth of penetration of edge effects with exactitude due to gradual changes in topography, soil composition, and heterogeneity in vegetation distribution from the edge into interior forest (Laurance et al., 1998; Harper et al., 2005; Murcia, 1995). In this study, I determined the depth of edge effects at 400 m, a distance that fell within the ranges found in other studies. Olupot (2009) found that edge effects penetrated up to 300 m inside the forest but could still be detectable at 1000 m in the interior of the Bwindi forest. Elsewhere, following the creation of forest edge, large trees die off within 300 m of the forest edge (Laurance et al. 2000) due to increased penetration of sunlight, wind, temperature, vapor pressure deficit, and availability of photosynthetically active radiation to the understory (Kapos et al., 1993).

For Bwindi, I speculate that the additional impact on the forest structure of recent logging activities (until 1991) have an additive impact on the edge effects experienced in Bwindi forest. The age of forest edges has also been considered in interpreting the depths of edge effects. For example, Lovejoy et al. (1986) and Rodrigues (1998) suggested that tree densities might be lower on the edge than in interior forest soon after deforestation but the situation might reverse with time. In young logged forest, edge effects might extend as far as 5-10 km into intact forests (Curran et al., 1999), while in older forest these effects might cover shorter distances (Harper et al., 2005).

Canopy openness and ground vegetation cover have both been used to characterize habitat types in the Bwindi forest (Nkurunungi et al., 2004; Ganas et al., 2004; Ganas et al., 2009). Due to edge effects, I found that edge forest zones (< 400 m) had a higher canopy cover than the interior zones (> 400 m). Aubréville (1938) claimed that certain tropical forests can be defined as a mosaic of former gaps, which appears to be applicable to the Bwindi forest, which is composed of former, permanent, and newly created forest gaps. In some quadrats the canopy cover fell below 50%, a criterion that Wieczkowski & Mbora (2000) have used to classify forest habitat types in the fragmented Tana River Primate Reserve in Kenya. In Bwindi forest, such canopy openness was an indication that the study area could be considered secondary forest in an early successional stage. Additionally, by combining vegetation data from edge zones (< 400 m) or interior zones (> 400 m), I found that species area curves did not reach the asymptotes because of small sample sizes. However looking at the curves, the interior forest seemed to support less species richness but more habitat types, including marsh, riverine, open gaps, and regenerating, mixed and mature forests than the edge.

The current condition of the Bwindi forest in the proximity of the matrix and the patterns in species and habitat distribution are likely due to the combined influence of logging and edge effects, causing shifts in plant community composition and successional dynamics, changes in species diversity, and an increase in tree mortality rates that are exacerbated by global and local climate changes (Laurance et al., 1998; Laurance et al., 2001b; Nascimento & Laurance, 2004; Laurance et al., 2000; Olupot, 2009).

CONCLUSION

Edge effects in Bwindi followed non-monotonic patterns (wave-like) in species distribution and microhabitat characteristics, most likely due to the additive influence of the history of logging in the area, and the persistent human disturbances which penetrate considerable distances into the forest from the edge. According to Murcia (1995), it may be impossible to separate patterns in terrain depressions or elevations or soil discontinuities with edge effects. In addition to edge parameters such as matrix and forest type, edge age, orientation, and formation, the detrimental impact of selective logging has had an impact on the interior forest, creating early successional habitats.

More systematic studies focusing on edge-related variables (i.e. age, orientation, disturbance, individual species distribution, etc.) should be undertaken to delineate how much logging and how far exposure to forest edge effects have affected microhabitat structure and composition in the Bwindi forest. By determining the depth of abiotic, biotic, and anthropogenic effects on species distribution and habitat structure from the forest edge, edge effect studies will be able to summarize key priorities for landscape conservation, including more involvement by local communities. In Bwindi, most anthropogenic disturbances that are working in cadence with edge effects have been found in Multiple Use Zones (MUZ), where local people are allowed to set beehives or collect medicinal plants (Bitariho et al., 2006). It is virtually impossible to set sustainable limits in MUZs; this is the main reason why Muir (1991) suggested that cultivating alternative sources for poles and firewood outside of indigenous forest can be over ten times cheaper than the cost of an intensive monitoring program for sustainable use of that resource in the park. The challenge around Bwindi is that there is no more land for non-crop plantations.

Edge effects on habitat structure and plant species were easily detectable in vegetation canopy cover and density and distribution of understory vegetation species, especially terrestrial herbs and density and distribution of pioneer forest tree species. Patterns in edge vegetation canopy cover and plant species distribution have resulted mostly from edge effects, the legacy of past logging activity, and current pole cutting and wood collection, including trampling by a local human population that frequents the park at high density. If such overwhelming human activities were reduced on the edges of the park and if the forest was allowed to some degree to colonize the closest surrounding matrix outside the park, a softer edge (Forman, 1995) could slowly replace the current hard edge and minimize edge effects on species and their habitat along the boundary and in the interior of the Bwindi forest. Ultimately, biotic factors other than those explored in this study as well as abiotic factors such as microclimate need to be examined to completely characterize forest edge effects on the physiognomy and ecosystem behavior of Bwindi Impenetrable National Park.

LITERATURE CITED

Andrén H. 1995. *Effects of landscape composition on predation rates at habitat edges*. In Hansson L., Fahrig L. & G. Merriam. *Mosaic landscapes and ecological processes.* Chapman & Hall. London.

Aubréville A. 1938. *La forêt coloniale – Les forêts de l'Afrique Occidentale Française*. Société d'Éditions Géographiques, Maritimes et Coloniales. Paris.

Babaasa D. 2000. Habitat selection by elephants in Bwindi Impenetrable National Park, south-western Uganda. *African Journal of Ecology* 38: 116-122.

Babaasa D., Eliu G., Kasangaki A., Bitariho R. & A. McNeilage. 2004. Gap characteristics and regeneration in Bwindi Impenetrable National Park, Uganda. *African Journal of Ecology* 42: 217-224.

Bitariho R., A. McNeilage, D. Babaasa, & R. Barigyira. 2006. Plant harvest impacts and sustainability in Bwindi Impenetrable National Park, S.W. Uganda. *African Journal of Ecology* 44: 14-21.

Bossart J.L. & E. Opuni-Frimpong. 2009. Distance from edge determines fruit-feeding butterfly community diversity in Afrotropical forest fragments. *Environment Entomology* 38: 43-52.

Broadbent E.N., G.P. Asner, M. Keller, D.E. Knapp, P.J.C. Oliveira & J.N. Silva. 2008. Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. *Biological Conservation* 141: 1745-1757.

Brower J.E., J.H. Zar & C.N. von Ende. 1997. *Field and laboratory methods for general ecology* (4th ed.). WCB/McGraw-Hill companies. USA.

Butynski T.M. & J. Kalina. 1993. Three new mountain parks for Uganda. *Oryx* 27: 214-224.

Butynski T.M. 1984. *Ecological survey of the Impenetrable (Bwindi) forest, Uganda, and recommendations for its conservation and management*. New York Zoological Society. New York.

Chen J., Franklin J.F. & T.A. Spies. 1992. Vegetation responses to edge environments in old-growth Douglas-fir forests. *Ecological Applications* 2: 387-396.

Curran L.M., I. Caniago, G.D. Paoli, D. Astianti, M. Kusneti, M. Leighton, C.E. Nirarita & H. Haeruman. 1999. Impact of El Niño and Logging on Canopy Tree Recruitment in Borneo. *Science* 286: 2184-2188

Duncan R.S. & C.A. Chapman. 2003. Tree-shrub interactions during early secondary forest succession in Uganda. *Restoration Ecology* 11: 198-207.

Ewers R.M. & R.K. Didham. 2007. The effect of fragment shape and species' sensitivity to habitat edges on animal population size. *Conservation Biology* 21: 926-936.

Ewers R.M. & R.K. Didham. 2008. Pervasive impact of large-scale edge effects on a beetle community. *Proceedings of the National Academy of Sciences* 105: 5426-5429.

Forman R.T.T. 1995. *Land mosaics: the ecology of landscapes and regions*. Cambridge University Press. New York.

Fritz R. & G. Merriam. 1996. Fencerow and forest edge architecture in eastern Ontario farmland. *Agriculture, Ecosystems and Environment* 59: 159-170.

Ganas J., M.M. Robbins, J.B. Nkurunungi, B.A. Kaplin & A. McNeilage. 2004. Dietary Variability of Mountain Gorillas in Bwindi Impenetrable National Park, Uganda. *International Journal of Primatology* 25: 1043-1074.

Ganas J., J.B. Nkurunungi & M.M. Robbins. 2009. Temporal and spatial variability of herbaceous vegetation consumed by mountain gorillas in an Afromontane rainforest. *Biotropica*. 41: 37-46.

Hamilton A. 1984. *Deforestation in Uganda*. Oxford University Press. Nairobi. Kenya.

Harper K.A., E. Macdonald, P.J. Burton, J. Chen, K. Brosofske, S.C. Saunders, E.S. Euskirchen., D. Roberts, M.S. Jaiteh & P.-A. Esseen. 2005. Edge influence on forest structure and composition in fragmented landscapes. *Conservation Biology* 19: 768-782.

Howard P.C. 1991. *Nature conservation in Uganda's tropical forest reserves*. IUCN Gland. Switzerland.

Kapos V., G. Ganade, E. Matsui & R.L. Victoria. 1993. Ə^{13}C as indicator of edge effects in tropical rainforest reserves. *Journal of Ecology* 81: 425-432.

Krebs C.J. 1989. *Ecological Methodology*. Harper and Row Publishers. New York.

Lande R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* 76: 5-13.

Laurance W.F., D. Pérez-Salicrup, P. Delamonica, P.M. Fearnside, S. D'Angelo, A. Jerozolinski, L. Pohl & T.E. Lovejoy. 2001a. Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology* 82: 105-116.

Laurance W.F., Williamson, G.B., Delamonica, P., Oliveira, A., Lovejoy, T.E., Gascon, C. & L. Pohl. 2001b. Effects of a strong drought on Amazonian forest fragments and edges. *Journal of Tropical Ecology* 17, 771–785.

Laurance W. F., P.Delamonica, S. G. Laurance, H. L. Vasconcelos & T. E. Lovejoy. 2000. Rainforest fragmentation kills big trees. *Nature* 404: 836–836.

Laurance W.F., L.V. Ferreira, J.M. Rankin-de Merona, S.G. Laurance, R. Hutchings & T.E. Lovejoy. 1998. Effects of forest fragmentation on recruitment patterns in Amazonian tree communities. *Conservation Biology* 12, 460-464.

Lehman S.M., A. Rajaonson & S. Day. 2006. Edge effects and their influence on lemur density and distribution in Southeast Madagascar. *American Journal of Physical Anthropology* 129: 232-241.

Lemmon R.E. 1957. *Forest densiometers*. Bartlesville. Oklahoma. USA.

Lovejoy T.E., R.O. Bierregaard Jr., A.B. Rylands, J.R. Malcolm, C.E. Quintela, L.H. Harper, K.S. Brown, Jr., A.H. Powell, H.O.R. Schubart & M.B. Hays. 1986. *Edge and other effects of isolation on Amazon forest fragments*. In Soulé M.E. (Ed.). *Conservation biology: The science of scarcity and diversity.* Sinauer Associates, Inc. Sunderland. Massachusetts. Pp. 257-285.

Matlack G.R. 1993. Microenvironment variation within and among deciduous forest edge sites in the eastern United States. *Biological Conservation* 66: 185-194.

Muir D.P. 1991. *Indigeneous forest utilization in Kwazulu: a case study of the Hlatikulu forest, Maputaland.* Thesis. University of Natal. Pietermaritzburg.

Murcia C. 1995. Edge effects in fragmented forests: implications for conservation. *Tree* 10: 58-62.

Nascimento H. E. M. & W. F. Laurance. 2004. Biomass dynamics in Amazonian forest fragments. *Ecological Applications* 14: 127–138.

Newmark W.D. 2001. Tanzanian forest edge microclimatic gradients: Dynamic patterns. *Biotropica* 33: 2-11.

Nkurunungi J.B., J. Ganas, M.M. Robbins & C.B. Stanford. 2004. A comparison of two mountain gorilla habitats in Bwindi Impenetrable National Park, Uganda. *African Journal of Ecology* 42: 289-297.

Olupot W. 2004. *Boundary edge effects in Bwindi Impenetrable National park*. Institute of Tropical Forest Conservation. Uganda.

Olupot W. 2009. A variable edge effect on trees of Bwindi Impenetrable National Park, Uganda, and its bearing on measurement parameters. *Biological Conservation* 142: 789-797.

Olupot W., C.A. Chapman. 2006. *Human encroachment and vegetation change in isolated forest reserves: the case of Bwindi Impenetrable National Park, Uganda*. In: Laurance, W.F. & C.A. Peres (Eds.). *Emerging Threats to Tropical Forests*. The University of Chicago Press. Chicago. Pp. 127-142.

Pomeroy D.E. 1990 (Ed.). *Conservation of biodiversity in Uganda*. Proceedings of Second Conservation Forum. Kabarole District. Uganda.

Rees M., P.J. Brubb & D. Kelly. 1996. Quantifying the impact of competition and spatial heterogeneity on the structure and dynamics of a four-species guild of winter annuals. *American Naturalist* 147: 1-32.

Ries L., R.J. Fletcher, J. Battin & T.D. Sisk. 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annual Review of Ecology, Evolution, and Systematics* 35: 491-522.

Rodrigues E. 1998. *Edge effects on the regeneration of forest fragments in south Brazil*. Dissertation. Harvard Univesity. USA.

Sanderson E.W., M. Jaiteh, M.A. Levy, K.H. Redford, A.V. Wannebo & G. Woolmer. 2002. The human footprint and the last of the wild. *Bioscience* 52: 891-904.

Schmidt W. 2005. Herb layer species as indicators of biodiversity of managed and unmanaged beech forests. *Forest Snow and Landscape Research* 79: 111-125.

Stamps J.A., M. Buechner. & V.V. Krishnam. 1987. The effect of edge permeability and habitat geometry on emigration from patches of habitat. *American Naturalist* 129: 533-552.

Tabarelli M., Lopes A.V. & C.A. Peres. 2008. Edge-effects drive tropical forest fragments towards an early-successional system. *Biotropica* 40: 657-661.

UNEP-WCMC. 2003. *Protected areas and world heritage: Bwindi Impenetrable National Park*. http://www.unep-wcmc.org/sites/wh/bwindi.html downloaded on 1 Sept 2008.

Wieczkowski J. & D.N.M. Mbora. 2000. Increasing threats to the conservation of endemic endangered primates and forests of the lower Tana River, Kenya. *African Primates* 4: 32-40.

Williams-Linera G. 1990a. Vegetation structure and environmental conditions of forest edges in Panama. *Journal of Ecology* 78: 3560373.

Williams-Linera G. 1990b. Origin and early development of forest edge vegetation in Panama. *Biotropica* 22: 235-241.

APPENDICES

Appendix 1. Tree and shrub species density per zone and per ha in the Bwindi forest.

			Distance zones sampled from edge				
Family	**Species**	**Type**	**15m**	**165m**	**315m**	**1000m**	**1700m**
Acanthaceae	*Mimulopsis arborescens*	Pioneer		3.18	6.37	38.22	20.28
Alangiaceae	*Alangium chinense*	Primary		38.22	12.74	15.92	40.57
Amaranthaceae	*Sericostachys scandens*	Pioneer			9.55		30.43
Anacardiaceae	*Rhus natalensis*	Pioneer	47.77	19.11	63.69		202.85
Apocynaceae	*Tabernaemontana holstii*	Pioneer		6.37			
Aquifoliaceae	*Ilex mitis*	Pioneer			6.37	3.18	20.28
Araliaceae	*Polycias fulva*	Pioneer	19.11	38.22	15.92	9.55	50.71
Asteraceae	*Vernonia africana*	Pioneer		3.18			
	Vernonia auriculifera	Pioneer		3.18			
Buddlejaceae	*Nuxia congesta*	Pioneer	70.06	15.92	25.48	19.11	81.14
Capparaceae	*Ritchiea albersi*	Pioneer	6.37	6.37	6.37		20.28
Caricaceae	*Carica papaya*	Pionieer		6.37			
Celastraceae	*Maytenus acuminata*	Pioneer	3.18	3.18	3.18	3.18	10.14
	Maytenus aethiopica	Pioneer		6.37		3.18	
	Rapannea rhododendroides	Pioneer	9.55	6.37		3.18	
	Salacia elegans	Pionieer				3.18	
Clusiaceae	*Symphonia globulifera*	Primary		6.37			
Connaraceae	*Connarus longistipitatus*	Pionieer				3.18	
Cupressaceae	*Cupressus sp.*	Pioneer	6.37				
Euphorbiaceae	*Alchornea hirtella*	Primary	31.85				
	Bridelia micrantha	Pioneer	19.11	60.51	25.48		81.14
	Croton macrostachys	Pioneer	3.18				0
	Erythrococca trichogyne	Pioneer		6.37	6.37		20.28
	Macaranga kilimandscharia	Pioneer	41.4	28.66	50.96	35.03	162.28
	Neoboutonia macrocalyx	Pioneer	19.11			44.59	
Flacourtiaceae	*Dovyalis macrocalyx*	Pioneer			3.18		10.14
Leguminosae	*Acacia sp.*	Pioneer	3.18				
	Albizia gummifera	Pioneer	6.37		3.18	6.37	10.14
Meliaceae	*Ekebergia capensis*	Primary		6.37	3.18	9.55	10.14
	Entandrophragma excelsum	Primary				31.83	
Melianthaceae	*Bersama abyssinica*	Pionieer	6.37	12.74	6.37	3.18	20.28
Monimiaceae	*Xymalos monospora*	Pioneer	70.06	200.64	187.9	63.69	598.4
Moraceae	*Ficus sp.*	Pioneer				3.18	0
	Myrianthus holstii	Pioneer	6.37	25.48	3.18		10.14
Myricaceae	*Agauria salicifolia*	Pioneer	22.29	3.18	31.85	9.55	101.42
	Myrica salicifolia	Pioneer	15.92	12.74			
Myrsinaceae	*Maesa lanceolata*	Pioneer	22.29	9.55	35.03	19.11	111.57
Myrtaceae	*Sygigium cordatum*	Primary	9.55				
Myrticaceae	*Syzigium guineense*	Primary	31.85	12.74	60.51	3.18	192.71
Olacaceae	*Strombosia scheffreri*	Primary		3.18	3.18	12.74	10.14
Oleaceae	*Olea capensis*	Primary			3.18	31.85	10.14
Olinaceae	*Olinia usambarensis*	Primary		3.18		15.92	

Family	**Species**	**Type**	**15m**	**165m**	**315m**	**1000m**	**1700m**
Pittosporaceae	*Pittasporum mannii*	Pionieer			3.18		10.14
Podocarpaceae	*Podocarpus milinjianus*	Primary	35.03			31.85	
Ptoteaseae	*Faurea saligna*	Pioneer	19.11	6.37	12.74	15.92	40.57
Rhizophoraceae	*Cassipourea sp.*	Primary				127.32	
Rosaceae	*Prunus africana*	Primary	6.37	22.29	15.92	3.18	50.71
Rubiaceae	*Galiniera coffeoides*	Pioneer	73.25	95.54	19.11	9.55	60.85
	Oxyanthus speciosus	Pioneer		3.18			
	Psychotria kirkii	Pionieer	3.18			3.18	
	Psychotria mahonii	Pionieer	19.11	31.85	0	60.51	
	Rytginia beniensis	Pionieer			3.18		10.14
	Rytiginia kigeziensis	Primary	3.18	15.92	3.18	6.37	10.14
	Rytiginia ruwnzoriensis	Primary		3.18	12.74	31.85	40.57
	Unidentified 1	Pioneer		3.18	3.18		10.14
Rutaceae	*Clausena anisata*	Pioneer			6.37		20.28
Sapindaceae	*Allophyllum abyssinica*	Pioneer	3.18	41.4	25.48	44.59	81.14
	Allophyllum macrobotrys	Pioneer				31.83	
Sapotaceae	*Chrysophyllum albidium*	Primary		6.37	3.18	0	10.14
Sterculiaceae	*Dombeya goetzenii*	Pioneer	3.18	12.74	31.85	41.4	101.42
Theaceae	*Filcalhoa laurifolia*	Primary				139.15	
Ulmaceae	*Trema orientalis*	Pioneer	3.18			3.18	
Unknown	*Unidentified 2*	Pioneer		31.83			
Urticaceae	*Urera sp.*	Pioneer		3.18			

Appendix 2. Understory plant and seedling plant species density per m^2 per zone in the Bwindi forest.

			Understory density/m² per zone				
Family	**Species full**	**Life form**	**15m**	**165m**	**315m**	**1000m**	**1700m**
Acanthaceae	*Brillantasia nitens*	Herb					1.5
	Dicliptera laxata	Herb					2.1
	Justicia sp.	Herb	0.1				
	Justicia striata	Herb	4.1	1.7	6.5	3.2	7
	Mimulopsis solmsii	Vine	2.1	3.8	2.3	14.5	15
	Stanrogyne alboviolacea	Herb				1.6	
	Thunbergia alata	Herb			0.1		0.5
Alangiaceae	*Alangium chinense*	Tree	0.2	0.1			
Amaranthaceae	*Achyranthes aspera*	Herb	3.8	2.1	0.7	0.6	0.7
	Celosia stelmaninia	Herb			0.3		
	Sericostachys scandens	Vine	0.1	0.1	0.3	1.5	1.5
Aquifoliaceae	*Ilex mitis*	Tree			0.1		
Araceae	*Culcasia falcifolia*	Shrub	1.4		1.6		
Asclepiadaceae	*Periploca linearifolia*	Herb	0.1				
	Praquetina sp.	Herb				1.4	
	Asplenium sp.	Fern	9.4	17.1	34	9.7	2.7
Asteraceae	*Crassocephalum rubens*	Herb	2.5	1	1.3	0.6	0.8
	Vernonia calongansis	Shrub		0.2			
	Vernonia lasiopus	Shrub	0.4	0.2	0.4	0.6	0.2
Balsaminaceae	*Impatiens sp.*	Herb			0.5	0.1	0.3
Basellaceae	*Basella alba*	Herb		0.3			0.7
Campanulaceae	*Monopsis stellarioides*	Herb	0.8	0.1	1.7	0.2	0.6
Caricaceae	*Carica papaya*	Tree		0.1			
Caryophyllaceae	*Drymaria cordata*	Herb	5.8	0.7	0.2	0.5	4.4
Celastraceae	*Maytenus senegalensis*	Shrub		0.1	0.4		
	Pristimera graciliflora	Herb	0.7	0.3	0.9	0.8	0.1
	Salacia leptoclada	Vine					0.1
Clusiaceae	*Symphonia globulifera*	Tree	0.2				
Colchicaceae	*Gloriosa superba*	Herb	0.1		0.2		
Commelinaceae	*Commelina sp.*	Herb	4.2	0.5	0.5	0.8	0.6
Compositae	*Mikania cordata*	Vine					0.1
Concolvulaceae	*Ipomea sp.*	Herb	2.3	1.7	1.3	0.2	4.4
Connaraceae	*Connarus longistipitatus*	Shrub		0.1	0.1	0.1	
Crassulaceae	*Kalanchoe densiflora*	Herb	1.7			0.1	
Cucurbitaceae	*Coccinia grandis*	Herb		0.5			
	Coccinia mildbraedii	Herb				0.1	
	Momordica charantia	Herb	0.1				0.3
	Momordica pteridium	Herb		0.1	0.1	0.1	2.5
Cyatheaceae	*Cyathea manniana*	Fern		0.1	0.1	0.2	1
Cyperaceae	*Cyperus sp.*	Herb	0.1		0.1		
Dennstaedtiaceae	*Pteridium sp.*	Fern	0.7		0.1	1.4	1.6
Euphorbiaceae	*Alchornea hirtella*	Vine					0.1
	Bridelia micrantha	Tree	0.1	2.4	0.7		
	Clutia abyssinica	Shrub	1.3	0.3		0.5	
	Erythrococca trichogyne	Shrub		0.6	0.4		

Family	**Species full**	**Life form**	**15m**	**165m**	**315m**	**1000m**	**1700m**
	Macaranga kilimandscharia	Tree	0.1		0.3		0.1
	Neoboutonia macrocalyx	Tree				0.2	0.5
	Phyllanthus fischeri	Herb	2.3	0.9	1.1		
Fabaceae	*Desmodium rependum*	Herb		1.2	1.5	0.2	0.6
Geraniaceae	*Geranium arabicum*	Herb					0.2
Labiatae	*Orthosiphon australis*	Herb	1.9	4	0.6	0.1	1
	Plectranthus luteus	Herb	3.5		0.3	4.3	
Lamiaceae	*Plectranthus albus*	Herb	2.8	0.6		0.4	1.4
	Plectranthus edulis	Herb	2			1.2	1.6
Leguminosae	*Albizia gummifera*	Tree	1	0.1	0.2		
	Dolichos sp.	Herb	0.1				
	Pterolobium sp.	Herb	0.3	1	0.5		
Malvaceae	*Kosteletzkya adoensis*	Herb				0.1	
	Pavonia urens	Herb	0.1	0.3			
Monimiaceae	*Xymalos monospora*	Tree	0.3	1.1	1.8	0.1	0.1
Moraceae	*Myrianthus holstii*	Tree			0.1		
Myricaceae	*Agauria salicifolia*	Tree		0.3			
Myrsinaceae	*Embelia schimperi*	Herb			0.1		
	Maesa lanceolata	Tree		0.1			0.7
Olacaceae	*Strombosia scheffreri*	Tree				0.2	
Oleaceae	*Jasminum eminii*	Herb	0.5				
Oliniaceae	*Olinia usambarensis*	Tree	0.6				
Passifloraceae	*Adenia sp.*	Herb	0.1	0.4		0.1	
Phytolaccaceae	*Phytolacca dodecandra*	Herb					0.1
Piperaceae	*Piper capense*	Herb	0.2	3.5	0.9	0.7	0.1
Pittosporaceae	*Pittasporum mannii*	Tree		0.1			0.1
Poaceae	*Panicum sp.*	Herb	113.3	29.1	8.8	36.3	17.5
Podocarpaceae	*Podocarpus milanjianus*	Tree				0.1	0.8
Polygalaceae	*Securidaca welwitschii*	Vine	2.1	0.6		0.6	0.6
Polygonaceae	*Polygonum salicifolium*	Herb	0.1				
	Rumex abyssinicus	Herb	0.1				
Pteridaceae	*Pteris sp.*	Fern	0.1	0.1	0.6	0.1	0.2
Ranunculaceae	*Ranunculus multifidus*	Herb	0.3				
Rhizophoraceae	*Cassipourea sp.*	Tree				0.3	
Rosaceae	*Prunus africana*	Tree	0.7	22.8	1.9	0.3	0.1
	Rubus sp.	Vine	1.2	0.5	0.2	0.9	1.1
Rubiaceae	*Galiniera coffeoides*	Tree	0.4		0.4		
	Oxyanthus speciosus	Shrub				0.2	
	Pavetta ternifolia	Shrub			0.1		
	Pentas bussei	Herb	0.1	0.6			
	Psychotria kirkii	Shrub	1.9	0.4	0.3	0.6	0.3
	Psychotria monii	Tree		0.3	0.1	3.6	1.7
	Rutidea orientalis	Vine	1.3	0.7	1.4	0.2	
	Rytiginia beniensis	Tree	0.1	0.6		0.3	
	Rytiginia bugwensis	Tree	0.1	0.3			
	Rytiginia ruwenzoriansis	Tree		0.3	1.1	1.9	0.1
	Spermacoce princeae	Herb	0.1		1.2		
	UNK1	Shrub	0.1		0.1		

Family	**Species full**	**Life form**	**15m**	**165m**	**315m**	**1000m**	**1700m**
Rutaceae	*Clausena anisata*	Tree		0.1	0.5		
	Teclea nobilis	Tree					0.2
Sapindaceae	*Allophyllum abyssinica*	Tree	1.2	3	3.8	0.7	0.5
	Allophyllum macrobotrys	Tree				0.3	0.6
	Draceana laxissima	Vine	0.4			0.3	0.1
Sapotaceae	*Chrysophyllum albidum*	Tree				0.1	
Smilacaceae	*Smilax anceps*	Herb	0.1				
Sterculiaceae	*Dombeya goetzenii*	Tree					0.3
Tiliaceae	*Triumfetta green*	Herb	0.8	1.8		0.8	1.1
	Triumfetta sp2.	Vine	1	0.4	1.1	1.2	1.1
Unknown	*UNK2*	Herb	0.1				
	UNK3	Herb	0.1			0.1	
Urticaceae	*Droguetia iners*	Herb	0.3	0.8			
	Laportea aestuans	Herb					0.3
	Pilea holstii	Herb	0.1	0.1	0.2		2.9
	Urera sp.	Vine	0.1	0.1	1.2		0.9
Verbenaceae	*Clerodendrum sp.*	Vine	0.5	0.2	0.6	0.5	0.7
Vitaceae	*Cissus (arguta) oliveri*	Herb	0.4		0.4		0.1
	Cyphostemma bambuseti	Herb		0.1		0.3	
	Cyphostemma sp.	Herb					0.4

CHAPTER 3

EDGE EFFECTS ON RANGING AND FEEDING ECOLOGY IN L'HOEST'S MONKEYS (*CERCOPITHECUS LHOESTI*), A SEMI-TERRESTRIAL FOREST PRIMATE

ABSTRACT

Forest edge effects on l’Hoest’s monkeys (*Cercopithecus lhoesti*) were assessed by comparing the feeding ecology and habitat use of edge and interior groups in Bwindi Impenetrable National Park in southwestern Uganda. After habituating two groups for nine months, I began data collection in which I monitored movement patterns and recorded diet composition for 13 months. I sampled vegetation in the home ranges of both groups, in the interior and along the forest edge. The forest canopy was more open in the interior, while herbaceous vegetation density was highest along the forest edge. Both groups had a striking similarity in diet composition. The lack of major differences in habitat use by both groups may indicate that forest habitats along the edge and in the interior are relatively similar due to previous logging activities that extended from the edge to over 6 km inside the park. However, the edge group had a more diverse diet, including subsistence crop plant species such as beans, maize, and sorghum. The time that the edge group spent feeding on each food plant was correlated with the abundance of these species along the forest boundary, in contrast to the interior group, which foraged on plant food species regardless of their abundance. This is one of the reasons why the edge group had a short day path when they had invaded crops that are usually clumped in one place. Overall, due to edge effects, the edge group had a larger home range (70.84 ha) than the interior group (51.81 ha), and a longer mean daily path (edge: 2204 ± 254 m; interior: 1675 ± 303 m, n = 13 months). L’Hoest’s monkeys are therefore likely to expend more energy overall compared with groups in the interior forest to obtain food and avoid risks, but such energy may be paid off by feeding on items of relatively higher nutritional value such as crops.

KEY WORDS: *Cercopithecus lhoesti,* edge effects, secondary vegetation, ranging ecology, foraging behavior, crop raiding

INTRODUCTION

Rainforests globally are disappearing at an alarming rate, with net tropical deforestation exceeding 150,000 km^2 per year (FAO, 1993, Whitmore, 1997). Deforestation results in fragmentation and increased edge-affected forest, both of which have a significant influence on patterns of species abundance and distribution (Harris, 1984; Laurance & Bierregaard, 1997; Pimm & Raven, 2000). An immediate effect of forest fragmentation is the creation of new edges, interfaces between the original indigenous vegetation and land cover of a different type (Denyer et al., 2006). Edges between forest and non-forest habitats have become a widespread feature across tropical landscapes due mainly to human activities (Lidicker, 1999; Laurance et al., 2002). Forest edges undergo changes in microclimatic and biotic factors that affect the composition and distribution of species and the structure of edge microhabitats (Janson & Boinski, 1992). Edge and interior forest microhabitats generally differ in physiognomy and food production, which can influence species ranging behavior (Gathua, 2000). For example, pioneer plant species are often dominant on edges and in forest gaps in montane tropical forest (Brokaw, 1985; Babaasa et al. 2004). These pioneer species are believed to produce abundant new leaves that have high protein-to-fiber ratios (Coley & Barone, 1996).

As Lidicker (1999) has suggested, investigations of forest edge-related variations in the behavior of animal species can offer deeper understanding of landscape level processes. Comparing the ranging patterns and feeding ecology of forest edge and interior forest species could provide valuable information about edge effects and habitat quality for the conservation of threatened species (Zanette et al., 2000; Menon & Poirier, 1996). Few studies have looked at forest edge effects on the distribution and density of primate species (Gathua, 2000; Lehman et al., 2006 a, b & c). Such studies are timely, since the expansion of edge forest results in the loss of habitat and may cause local extinction of interior specialist species (Merriam & Wegner, 1992; Woodroffe & Ginsberg, 1998). Such loss is especially important in biodiversity hotspots and refugia (Terborgh, 1992; Stevens & Husband, 1997).

The survival strategies of species living in edge-affected habitat are determined by a complex set of variables. Animals living along forest edges may have difficulties balancing energy gained and spent while foraging due to risks associated with edge habitat, and to structural or vegetation composition differences in edge-affected habitat. Lower food availability and density may result in longer day paths, suggesting that individuals have to travel more to meet their nutritional requirements (Gillespie & Chapman, 2001).

Home range size may also increase in lower-quality habitats and decrease as food sources become more abundant (Dunbar, 1988; Boonratana, 2000; Passamani & Rylands, 2000; Siex, 2003). The distribution, quality, and quantity of food are among the major extrinsic parameters that may radically affect the ranging behavior and movement patterns of primate groups (Enstam, 2002). For example, differences in the nutritional content of food species among different habitats are believed to influence the behavior of gorilla groups (Nkurunungi et al., 2004; Ganas et al., 2004). Furthermore, animals living on forest edges may come into proximity with human settlements, which can create changes in behaviors (Cowlishaw, 1998; Baker, 2004; Andama, 2007); these animals have been considered pest or problem species due to these interactions (Richard et al. 1989). In such ‘areas of tension’, Stevenson and Husband (1997) demonstrated that forest edges were sink areas for small mammal populations that depend on immigration for persistence. This may also apply to large mammals, including certain primate species which may become locally extinct due to potential sub-optimal characteristics of forest edges (Wong & Sicotte, 2007). Before the extinction of animal species, however, forest edges would progressively inflict subtle effects on the movements and foraging ecology of these animals.

This study aimed at finding out how the ranging and foraging behavior of l’Hoest’s monkey (*Cercopithecus lhoesti*) is affected by forest edges and what factors influence their movement patterns in the Bwindi Impenetrable National Park in Uganda. Bwindi Impenetrable National Park is a biodiversity hotspot and a refugium in which edge effects are of immediate conservation concern. The habitat of many primate species in the Bwindi forest has been compressed and edge forests are highly disturbed (McNeilage et al., 2001; Olupot, 2004). I investigated edge effects on the ranging and foraging patterns of l’Hoest’s monkey by examining differences and similarities between a forest edge group that dwelled along the park boundary and an interior group that resided between 600 m and 2200 m away from the edge towards the interior of the park. In this chapter, I highlight the ways in which seasonal food resources, including local subsistence crops, affect the ranging and foraging patterns of l’Hoest’s monkeys on forest edges.

METHODS

Study site

Bwindi Impenetrable National Park, in southwestern Uganda ($0^{\circ}53'$ - $1^{\circ}08'$S and $29^{\circ}35'$ - $29^{\circ}50'$E), is located in the Albertine Rift, a biodiversity hotspot and montane glacial refugium (Hamilton, 1988). Bwindi has been identified as one of the few large expanses of forest in East Africa where lowland and montane vegetation communities meet and as the most important forest for biodiversity conservation in Uganda (Howard, 1991). The 321 km^2 of forest is characterized by a high degree of plant, mammal, and avian endemism (Bibby et al., 1992). Over 120 mammal species, including primates, carnivores, and ungulates, coexist and interact with each other in the Bwindi forest. Gorillas (*Gorilla gorilla beringei*) and chimpanzees (*Pan troglodytes*) are believed to occur mainly in the interior forest, while monkeys, namely l'Hoest's' monkey (*Cercopithecus lhoesti*), olive baboons (*Papio anubis*), red-tailed monkey (*Cercopithecus ascanius*), blue monkey (*Cercopithecus mitis*), and black and white colobus (*Colobus guereza*) are more often found on the forest periphery and occasionally forage on local crops (Butynski, 1984; McNeilage et al, 2001; Baker, 2004; Andama, 2007).

The climate in Bwindi is characterized by two wet season peaks, with rains from March to May and September to November, with dry seasons in between. The period from September to November typically receives the greatest amount of rainfall, while June to August is the longest and most severe dry season (Baker, 2004). Compared with other highland forests in Uganda, Bwindi has the highest mean of 148 days (40%) of rain per year (Tukahirwa & Pomeroy, 1993). The average annual rainfall at the Ruhija research station in Bwindi is 1450 mm (Bitariho et al, 2006). The mean annual temperature is 13˚C and the mean daily minimum and maximum are 7˚C and 20˚C respectively (Butynski, 1984).

Logging in Bwindi ceased in 1991, when the forest was declared a national park. Currently, human activities inside the park have been reduced significantly due to increased protection by the Uganda Wildlife Authority (UWA). During my study, members of the local Kitojo community (*ca* 50 people) were involved in a campaign to eradicate from the park exotic trees including *Eucalyptus*, pine, and cypress found along the forest edge, along roads, and inside the park where this study was conducted.

Ranging and foraging data

Field work was conducted from October 2005 to September 2007. The first nine months were dedicated to finding and habituating two groups of l'Hoest's monkeys, an edge group and an interior group with initial group sizes of 36 and 18 individuals respectively. The edge group ranged along the forest edge up to 400 m inside the park, and the interior group ranged from 600 m to approximately 2.2 km away from the edge into the interior of the forest. Behavioral data were collected between July 2006 and September 2007. Every 30 the 'estimated center of mass' (Cords, 1984; Kaplin & Moermond, 2000) was recorded for group location using a Global Positioning System (GPS) unit (Raboy & Dietz, 2004). For each full-day follow, a ranging map of the l'Hoest's group was created using ArcView 3.2 (see Siex, 2003). The daily path length was determined based on the distance in meters between several GPS locations linking two consecutive sleeping sites. These daily paths were non linear and occasionally monkeys slept at the same site for several consecutive nights.

One field assistant and I followed each group for 4 to 6 days each month from 0730 to 1830 hours. I collected all behavioral data myself to avoid observer bias. I used instantaneous scan sampling at 5 minute intervals to record behavioral activities (Altmann, 1974; Martin & Bateson, 1986). Any activity sustained for at least 5 seconds was recorded for each individual during each group scan (Kaplin & Moermond, 2000). Each individual was recorded only once per scan, but could appear in successive scans. Each scan lasted two minutes with an intermission of three minutes that allowed me to keep up with the group and record ad libitum observations between scans. I recorded behavioral data on as many different individuals as possible (6 ± 3 individuals per scan on average from 14865 total scans for both groups) during a scan by frequently changing positions. I recorded the height (in meters) at which monkeys were feeding, categorized and identified to species (when possible) every food item (i.e. fruit, flowers, leaves, pith, sap), and used generic names for invertebrates and small animals that were consumed by l'Hoest's monkeys.

Vegetation sampling

I sampled vegetation within five zones based on distance from forest edge: 15 m, 165 m, 315 m, 1000 m, and 1700 m. Ten circular vegetation plots (10 m radius) were systematically located perpendicular to the forest edge at each zone, all within the home ranges of the monkey groups. Thus I had thirty vegetation plots inside the home range of the edge group and 20 within the interior group's home range; these latter 20 plots were collectively considered interior or control plots. All plots were located at least 100 m from one another. All plots were geo-referenced. Within the plots, all tree stems $\geq$ 5 cm diameter at breast height (DBH) were sampled and identified to species when possible.

The DBH of each tree stem was measured using a DBH tape (in cm). I also visually estimated the height of each tree stem (in m). For very tall trees, I used the ‘stick method’ to estimate the vertical height.

I calculated the dominance index of each tree species using relative frequency, relative density, and relative cover (basal area) of each species (Brower et al., 1997). I also calculated the Simpson’s diversity index $D=1-\Sigma [pi^2]$, where pi is a proportional cover of the i^{th} species in a plot, to examine differences in the abundance of terrestrial herbaceous vegetation (THV) and understory plant species in edge and interior forest.

I established four 1 m^2 quadrats at every 90^o from the north of each circular plot for a total of 120 quadrats on the edge and 80 in the interior forest. The percentage of ground vegetation cover was estimated using a 10 cm^2 frame and percentage canopy vegetation cover measured from the center of each quadrat using a densiometer. When possible, all herbs known to be eaten by l’Hoest’s monkeys were identified to species. Samples of unknown species were taken to the herbarium of the Institute of Tropical Forest Conservation (ITFC) at Ruhija in the Bwindi forest for identification. These data were used in comparing the distribution, plant species diversity, and habitat structure that may influence the foraging and ranging of the edge and interior groups of l’Hoest’s monkeys in Bwindi.

Data analysis

Differences in the composition of the diet of the edge and interior groups were determined with the Mann Whitney U-test and correlation relationships established between feeding records and plant food densities consumed. I calculated the similarity between the diets of both groups based on the formulas of Lande (1996) for community similarity. To compare monthly home ranges, ranging data from the first five days of each monthly group follow were considered in order to have an equal sample size (11 months) between both groups of l'Hoest's monkeys. Therefore, July and September 2006 were excluded from home range analysis because they both had less than 5 days of data per month for both groups. Fixed Kernel analysis, the extension of the home range analysis, was used to calculate 95% and 50% of the volume of the home ranges set at raster resolution of 70 in ArcView 3.2. Fixed Kernel is thought to give more accurate area estimates than MCP with very little bias and the lowest error (Seaman & Powell, 1996). Data were analyzed among 5 distant zones following an edge-interior gradient (15 m, 165 m, 315 m, 1000 m and 1700 m).

To compare with other studies, I created 100% minimum convex polygons (MCP) for the area used by each group (Kenward, 2001). Contrary to Kenward (2001), the monthly MCPs of l'Hoest's monkeys in Bwindi were smaller than the Fixed Kernel monthly estimates. Overall, however, the annual MCP was larger than the Fixed Kernel due to an increased number of peripheral locations recorded over 11 months (see Jenrich & Turner, 1969). Nevertheless, because MCP does not provide information on core areas (Kenward, 2001), I chose to use the Fixed Kernel to be able to interpret the home range use in both groups of l'Hoest's monkeys. I computed stepwise linear regression to identify major factors that influence daily path lengths and home ranges of l'Hoest's monkeys in Bwindi.

For the Analysis of Variance (ANOVA), the assumptions of normality were confirmed by the Kolmogov-Smirnov test. In addition, I computed the test of homogeneity in ANOVA. Percentages were arc-sin transformed to approximate a normal distribution when necessary (Sokal & Rohlf, 1981). I used the non-parametric Friedman test to compare between-group variables that had small sample sizes and were not normally distributed. These analyses were computed using SPSS 16.0 (SPSS Inc., Chicago, USA).

RESULTS

Plant species diversity and habitat structure

Seventy four families comprising a total of 143 plant species, including 53 tree, 57 herb, 16 shrub, 13 vine, and 4 fern species, were identified based on all plot and quadrat data in interior and edge forest combined. There was no significant difference in tree species dominance from edge to forest interior across the five distance zones (15 m; 165 m; 315 m; 1000 m and 1700 m) (ANOVA: $F_{4, 324}$=0.636, p=0.637) (Table 1). However, I found that tree density and mean tree height differed significantly across these distance zones ($F_{4, 49}$=3.32, p=0.02 and $F_{4, 49}$=2.65, p=0.04), but in no clear pattern (Figures 1 & 2). There was no significant difference in density distribution of understory plant species between the different distance zones from forest edge to interior ($F=_{4, 48}$ = 2.55, p = 0.053) (Appendix 1). However, a post hoc analysis showed that the density of understory plant species in the forest edge zone at 15 m was significantly higher than in zones 315 m, 1000 m and 1700 m (p = 0.009; 0.029 and 0.01 respectively). The edge around zone 15 m (5-25 m) was dominated by the herbs *Drymaria sp.*, *Commelina sp.*, *Asplenium sp.*, *Crassocephalum sp*, and *Panicum* sp.

Table 1. Dominance index of twenty most dominant tree, shrub and other flowering plant species of the study area in Bwindi Impenetrable National Park according to distance from forest edge.

Tree species	**15 m**	**165 m**	**315 m**	**1000 m**	**1700 m**
Xymolos monospora	70.29	201.16	188.44	63.91	9.61
Neoboutonia macrocalyx	19.20			44.74	137.61
Galiniera coffeoides	73.48	95.79	19.18	9.59	3.20
Macaranga kilimandscharia	41.55	28.74	51.11	35.15	16.02
Nuxia congesta	70.31	15.98	25.63	19.21	9.67
Psychotria mahonii	19.17	31.93		60.72	19.21
Rhys natalensis	47.93	19.17	63.88		
Dombeya goetzenii	3.26	12.79	31.95	41.57	28.82
Allophyllum abyssinica	3.20	41.53	25.55	44.73	
Syzygium guineense	31.96	12.77	60.69	3.20	
Bridelia micrantha	19.17	60.68	25.56		
Maesa lanceolata	22.37	9.63	35.16	19.24	9.63
Polyscias fulva	19.19	38.35	16.03	9.67	
Vernonia auriculifera		3.19			70.41
Podocarpus milanjianus	35.14			31.96	3.20
Agauria salicifolia	22.49	3.25	32.07	9.70	
Alchornea hirtella		38.32	12.79	16.06	
Faurea saligna	19.29	6.70	13.04	16.06	9.78
Rytiginia ruwenzoriansis		3.19	12.78	31.95	12.81
Mimulopsis arborescens		3.20	6.39	38.34	6.40

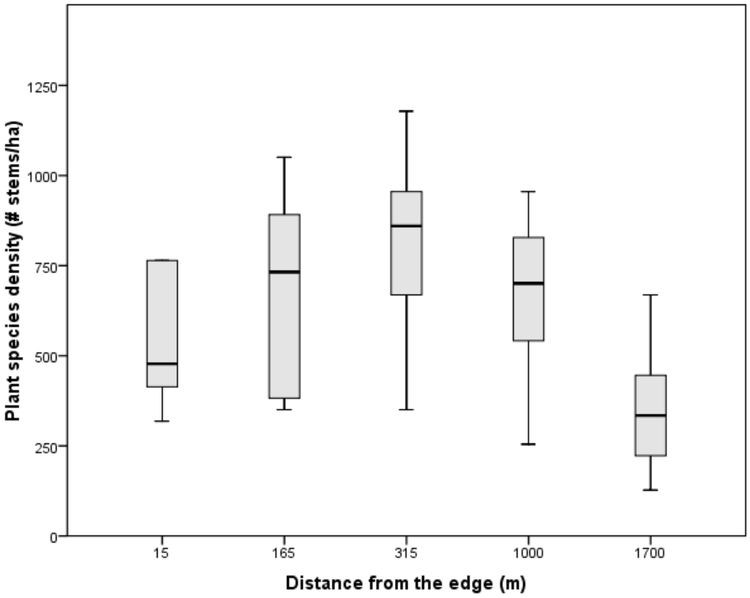

Figure 1. Distribution of plant species density across an edge-interior gradient. Zones 15 m, 165 m, 315 m, 1000 m and 1700 m had mean density ± standard deviation of 605 ± 305, 682 ± 252, 831 ± 227, 624 ± 279 and 408 ± 283 stems ha^{-1}.

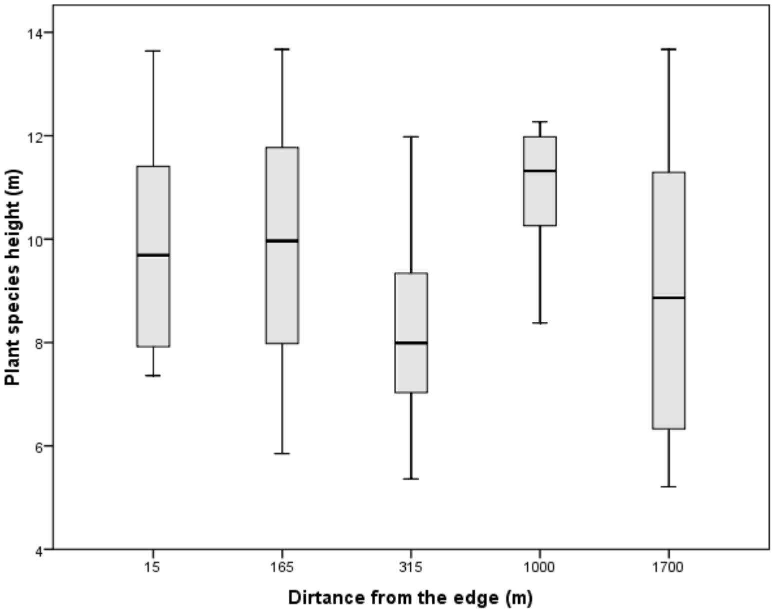

Figure 2. Distribution of plant species height across an edge-interior gradient. Zones 15 m, 165, 315, 1000, and 1700 m had mean height ± standard deviation of 9.76 ± 2.09, 8.84 ± 2.43, 8.28 ± 1.85, 10.52 ± 2.07, 9.05 ± 2.88 m respectively.

Edge effects had an influence on habitat characteristics and plant species distribution. The canopy cover was significantly different between zones ($F_{4, 47} = 3.437$, $p = 0.016$) (Figure 3). A post hoc test showed that zone 1700 m had a more open canopy than all edge zones. The plots located on the forest edge (< 400m from edge) had a higher mean percent canopy cover (87% ± 13) than the interior (> 400 m) plots (70% ± 25) ($F_{1, 46} = 9.314$, $p = 0.004$, Figure 4). The distribution of ground vegetation cover did not show any clear pattern but tended to decrease from the edge to 165 m towards the interior (Figure 5). Considering these results, I estimated the distance of penetration of edge effects at approximately 400 m into the interior forest vegetation.

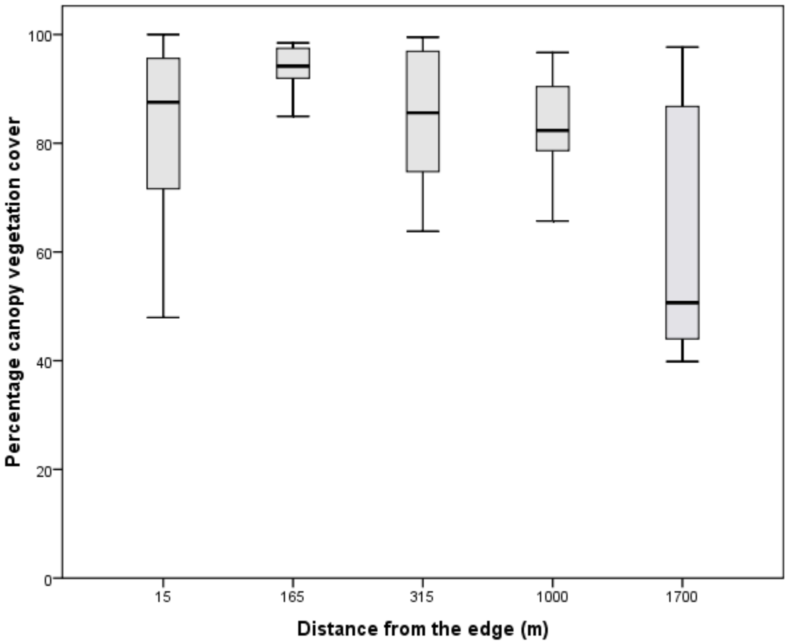

Figure 3. Percent canopy cover at distant zones from the forest edge towards the interior forest in Bwindi. Zones at 15 m, 165, 315, 1000 and 1700 m had mean percent canopy vegetation cover ± standard deviation of 82 ± 24, 82 ± 17, 93 ± 6, 85 ± 12, 76 ± 12 and 63 ± 24 respectively.

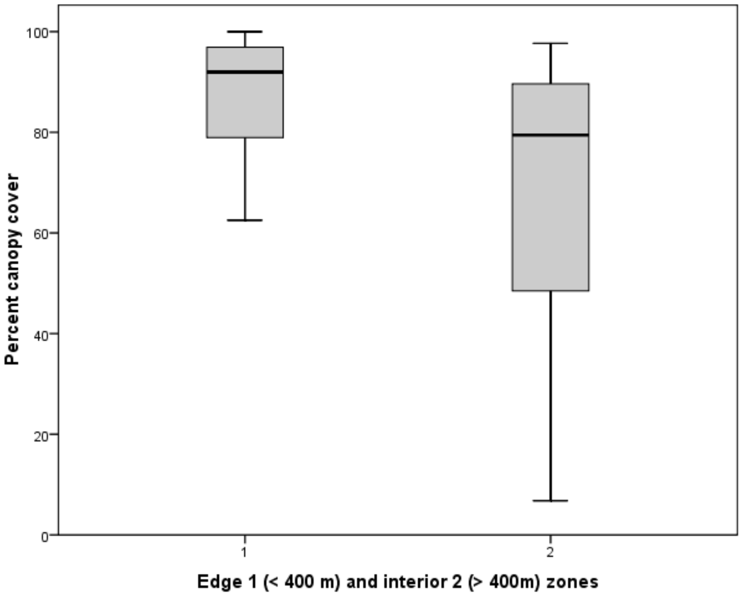

Figure 4. The canopy vegetation of the edge (< 400 m) was more covered that that of the interior forest in Bwindi (> 400 m) ($F_{1, 47} = 9.314$, $p = 0.004$).

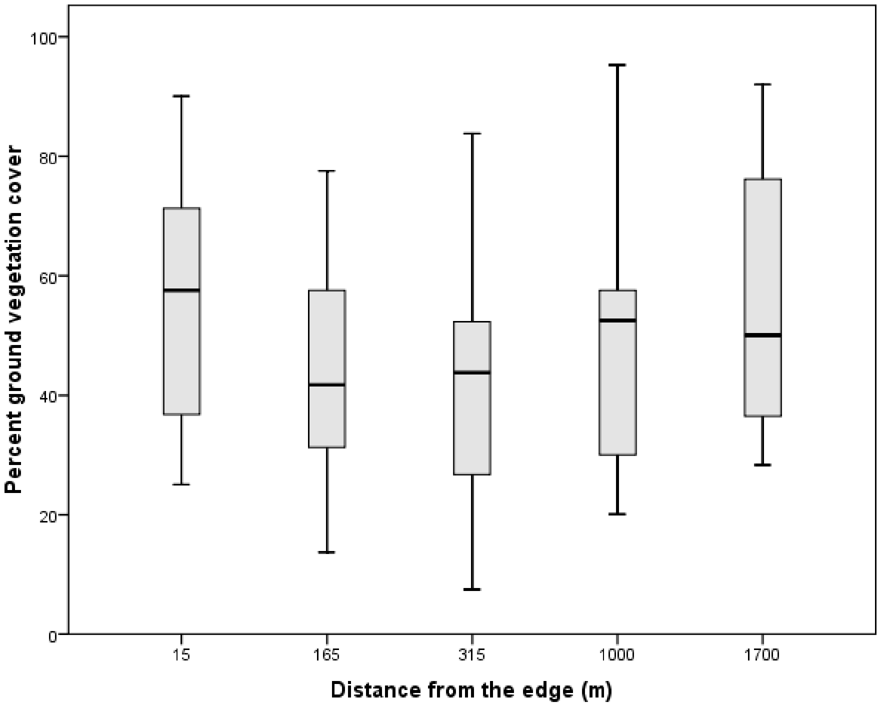

Figure 5. Percent ground vegetation cover at distant zones from the edge towards the interior forest in Bwindi. Zones at 15 m, 165 m, 315 m, 1000 m and 1700 m had mean percent ground vegetation cover ± standard deviation of 56 ± 21, 45 ± 20, 43 ± 23, 51 ± 22 and 56 ± 24 respectively.

Diet of the edge and interior groups

The Simpson diversity index of food species eaten by l'Hoest's monkeys was 0.954 and 0.947 for the edge and interior groups, respectively, with 99.2 % similarity in diet between the two groups. However, the edge group fed on significantly more food types and species than the interior group (Mann Whitney U = 27878, Z = -3.087 and p = 0.002, n= 257 food types) (Appendix 2). Two of the most abundant tree species upon which the monkeys foraged were *Xymalos monospora* (Apocynaceae) on the edge and *Neoboutonia macrocalyx* (Euphorbiaceae) in the interior forest. L'Hoest's monkeys fed on the pith of both species, especially during the dry season. Senescent and dry leaves of *Xymalos* and *Neoboutonia* species also hosted a variety of insects which the monkeys fed on. *Panicum sp.* was the most abundant terrestrial herbaceous vegetation (THV) species eaten by both l'Hoest's monkey groups. Overall, l'Hoest's monkeys consumed over 80% of the plant species sampled in vegetation plots in both the edge and interior, including 77% and 85% of THV species inventoried on the edge and in the interior group home ranges respectively.

There was no significant difference in the consumption of leaves (Friedman χ^2 = 3.77), flowers (Friedman χ^2 = 1.92), fruits (Friedman χ^2 = 0.08), invertebrates (Friedman χ^2 = 0.08), pith (Friedman χ^2 = 0.08) and seeds (Friedman χ^2 = 0.07) between the two groups ($p > 0.5$ for each test, n = 13 months). The edge group spent more time feeding on "other" food items such as tree bark, gum, meat of reptiles and rats, roots, and crops, than the interior group (Friedman χ^2=6.23, p = 0.01 and n = 13) (Table 2 and Appendices 2 & 3). I found a correlation between the abundance of food plant species located in the edge zone between 0 m and 50 m and the amount of time that the edge group of l'Hoest's monkeys spent feeding on them (Pearson r = 0.328, p = 0.002, n = 90). There was no significant correlation between food abundance and feeding records at the 165 m, 315 m edge zones and at the 1000 m, or 1700 m interior zones ($p > 0.5$ at all these different distances).

Table 2. Monthly feeding records (in %) on different food items for the edge (E) and interior (I) groups of l'Hoest's monkeys in the Bwindi forest. The percentage of leaves in this table includes terrestrial herbaceous vegetation (TVH) which accounted for 21.65% and 32.05% of the edge and interior group diets respectively.

Month	**Fruit**		**Invertebrate**		**Leaves**		**Pith**		**Seed**		**Flowers**		**Other**	
	E	**I**	**E**	**I**	**E**	**I**	**E**	**I**	**E**	**I**	**E**	**I**	**E**	**I**
Jul 06	43.1	44.6	33.1	9.0	9.8	28.8	2.1	1.3	0.3	11.4	10.2	1.9	1.4	3.2
Aug 06	60.1	59.4	8.3	11.7	20.6	21.5	3.1	0.5	1.1	1.6	2.4	1.2	4.6	4.2
Sept 06r	45.1	54.4	17.3	21.3	31.9	19.2	2.2	0.0	0.0	0.6	0.8	1.5	4.9	3.0
Oct 06	36.6	36.9	6.9	6.3	39.6	38.1	6.9	5.4	2.4	7.6	3.0	3.7	4.4	2.1
Nov 06	27.6	29.1	10.9	6.1	39.8	41.8	5.8	6.0	6.6	12.1	5.1	3.3	4.2	1.6
Dec 06	44.4	32.8	5.5	6.8	33.1	37.9	5.4	9.1	4.8	2.5	3.8	9.1	3.1	1.7
Jan 07	39.3	52.3	7.4	6.8	19.2	27.5	11.2	7.1	0.9	0.3	9.7	3.6	12.1	2.4
Feb 07	9.8	55.0	9.0	10.3	34.5	27.7	23.8	3.4	5.3	0.1	10.9	1.9	6.9	1.6
May 07	44.7	40.0	11.6	13.7	20.8	29.5	1.6	2.7	2.1	1.8	6.6	8.7	12.5	3.7
Jun 07e	29.5	33.6	7.7	10.2	20.7	31.2	6.1	5.3	10.0	2.2	19.2	10.8	6.8	6.7
Jul 07	20.4	12.4	14.8	13.6	28.4	43.5	6.6	12.4	5.7	1.4	19.4	9.2	4.6	7.6
Aug 07	19.6	16.4	14.5	8.1	26.0	51.4	6.6	10.8	3.5	2.1	24.4	8.7	5.3	2.5
Sept 07	26.6	14.8	18.0	10.6	26.8	53.1	4.4	5.8	0.6	1.2	17.3	10.9	6.4	3.6
Mean overall diet	**34.4 ± 16. 7**	**37.1 ± 15.9**	**12.7 ± 7.4**	**10.4 ± 4.2**	**27 ± 8.7**	**34.7 ± 10.6**	**6.6 ± 5.8**	**5.4 ± 3.8**	**3.3 ± 3**	**3.5 ± 4**	**10.2 ± 7.63**	**5.7 ± 3.8**	**5.9 ± 3.2**	**3.4 ± 1.9**

Feeding outside the park accounted for 4.8% of the total time that the edge group spent feeding throughout its home range. Of the total time spent outside the park, 88.5% was spent feeding on native vegetation and on the introduced Australian black wattle tree (*Acacia mearnsii*), while only 11.5% was devoted to feeding on crops. The native plant species eaten by the monkeys when outside the park included leaves of *Ipomea sp.*, species of ferns, *Panicum* spp. and *Commelina* spp., pith of *Secarida welwhitchi, Rhus natalensis,* and *Xymolus monospora*, and fruits of *Galiniera coffeoides, Alchornea hirtella*, *Maesa lanceolata*, and *R. natalensis*. These tree and herb species were found in active and fallow farms, pastures, and introduced tree plantations. Of the total time l'Hoest's monkeys spent feeding on crops, Irish potatoes represented 70.7%, sorghum 16.5%, beans 6%, sweet potatoes 3%, and maize 3%.

Home range size

The edge group generally had larger monthly home ranges than the interior group ($F_{1, 25} = 15.587$, $p = 0.001$). For 11 months of data collection, the Minimum Convex Polygon (MCP) (100%) of the edge group (85 ha) was greater than that of the interior group (66 ha) (Figure 6), and this was also true of home ranges estimated by Fixed Kernel methods (edge group: 70 ha; interior group: 52 ha) (Table 3). October 2006 was the only month when the home range of the edge group (28 ha) was smaller than that of the interior group (33 ha) (Table 3). In addition, dry seasons tended to have larger home ranges than wet seasons, especially for the edge group (Table 4).

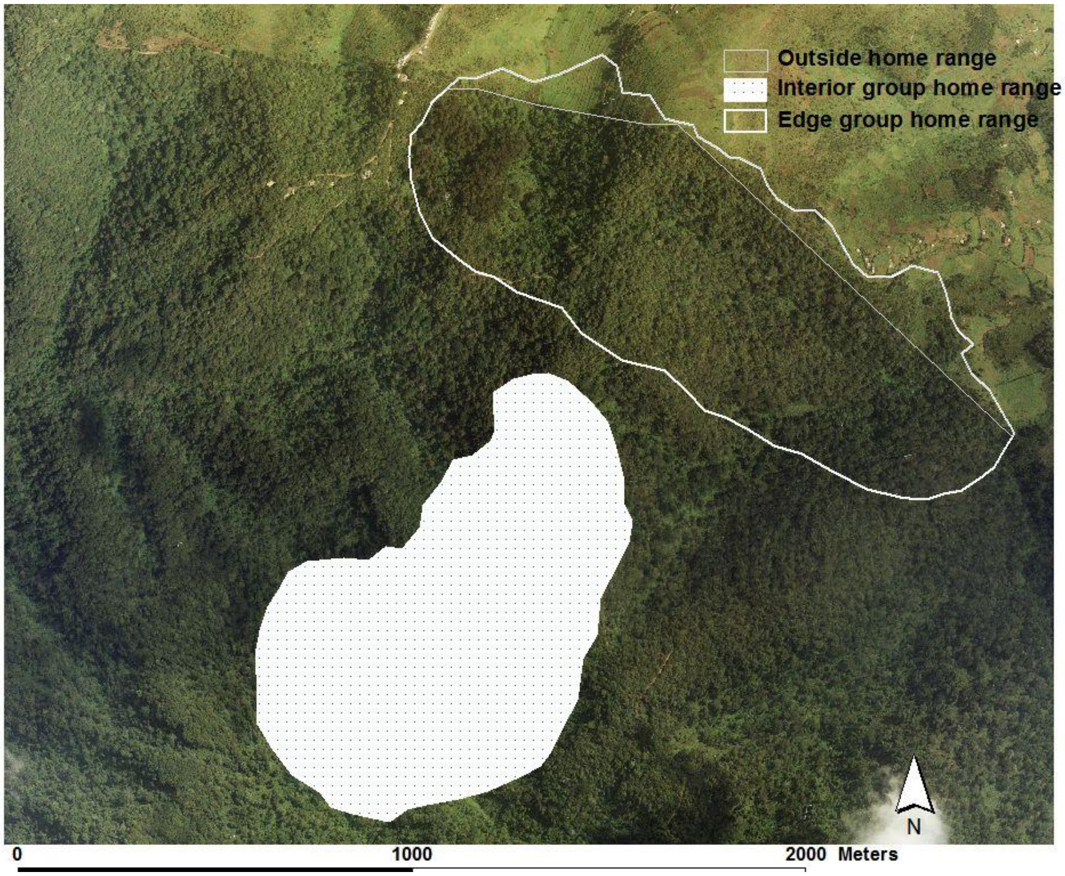

Figure 6. Edge and interior home ranges overlaid on an aerial photograph of the Bwindi forest. The map shows that the edge group home range extended outside the park boundary into cultivated fields.

Table 3. Monthly home ranges in ha for the edge and interior groups of l'Hoest's monkeys in the Bwindi forest.

Months	**Edge group**				**Interior group**			
	MCP (100%)	**# GPS Points (n)**	**Kernel (95%)**	***Kernel (50%)***	***MCP (100%)***	**# GPS points (n)**	***Kernel (95%)***	***Kernel (50%)***
Jul-06	31.86	55	36.45	10.45	37.83	37	36.92	10.23
Aug-06	40.95	104	41.14	12.2	37.65	51	36.54	10.11
Sep-06	35.32	38	40.35	11.96	24.66	62	24.74	6.76
Oct-06	25.3	76	28.25	8.35	32.67	64	33.59	8.79
Nov-06	38.94	86	46.82	14.94	29.52	71	33.2	11.36
Dec-06	49.54	89	55.17	15.81	38.75	83	40.05	11.43
Jan-07	65.04	89	78.62	24.68	24.93	55	27.86	7.82
Feb-07	46.38	65	49.14	12.09	23.1	60	20.79	5.74
May-07	42.39	61	53.91	14.61	31.42	80	36.85	9.95
Jun-07	33.56	68	40.81	10.78	27.56	52	34.88	10.2
Jul-07	36.33	59	45.96	11.6	32.55	68	36.75	10.24
Aug-07	37.53	69	48.92	13.79	27.08	54	33.38	9.56
Sep-07	42.27	59	57.2	16.98	33.96	61	36.18	11.46
Overall	**84.89**	**918**	**70.84**	**22.24**	**69.17**	**798**	**51.81**	**16.31**

Table 4. Seasonal differences in home range size of edge and interior groups in Bwindi Impenetrable National Park based on three different methods. Dry 1= Jun-Aug, Dry 2= Dec-Feb, Wet 1= Mar-May & Wet 2= Sept-Nov. with GPS (n) of 1894, 1427, 1034 and 2180 respectively.

Seasons	***Edge group***			***Interior group***		
	MCP (100%)	***Kernel (95%)***	***Kernel (50%)***	***MCP (100%)***	***Kernel (95%)***	***Kernel (50%)***
Dry 1	83.12	65.28	19.62	70.0	50.05	13.74
Dry 2	88.77	69.25	22.23	57.96	44.66	13.13
Wet 1	73.97	62.2	19.68	55.33	47.89	13.61
Wet 2	81.82	54.36	15.86	59.32	43.31	13.45

Variation in daily path length and the proportion of feeding records

The mean daily path length (DPL) of the edge group was greater than the mean DPL of the interior group (2174 m, s.d. = 467.57, n = 61 and 1666 m, s.d. = 416.44, n = 65, respectively) (ANOVA, $F_{1, 125} = 40.810$, $p \leq 0.0001$). October 2006 was the only month when the mean daily path was longer for the interior group than the edge group (Table 5). In general, l'Hoest's monkeys avoided paths used during previous days (Figures 7 & 8).

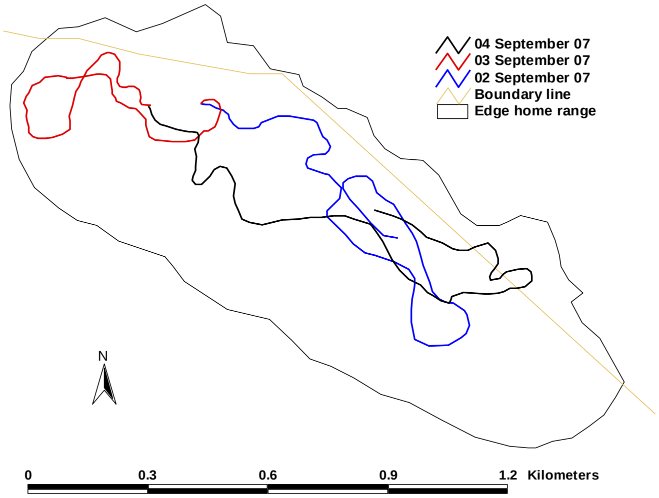

Figure 7. Three consecutive daily paths of the edge group of l'Hoest's monkeys on 2nd, 3rd & 4th September 2007 in the Bwindi forest.

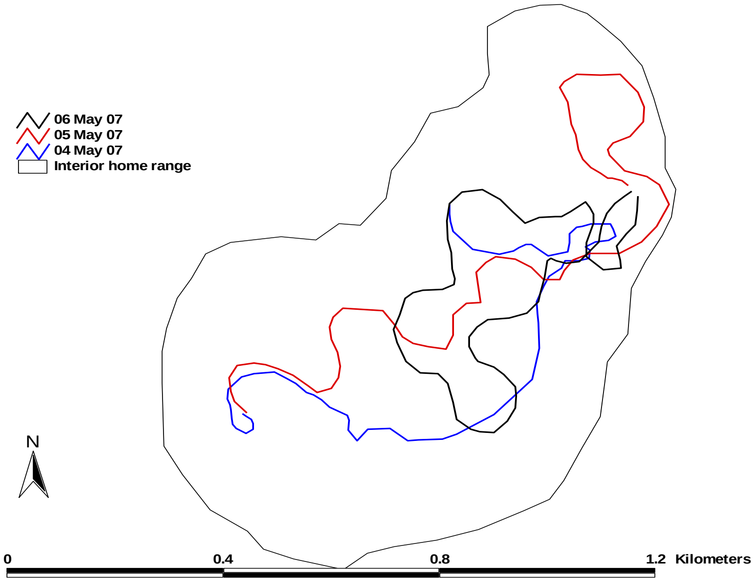

Figure 8. Three consecutive daily paths of the interior group of l'Hoest's monkeys on 3rd, 4th & 5th May 2007 in the Bwindi forest.

Table 5. Monthly mean and standard deviation (s.d.) of daily path lengths for the edge group and interior group of l'Hoest's monkeys in the Bwindi forest.

Month	**Edge group**		**Interior group**	
	Mean daily path length ± s.d. **(m)**	**n # of days**	**Mean daily path length** ± s.d. **(m)**	**n # of days**
Jul-06	2368 ± 277	2	1591 ± 172	3
Aug-06	2591 ± 549	5	1691 ± 559	5
Sep-06	2479 ± 445	4	2173 ± 343	2
Oct-06	1886 ± 296	6	1997 ±336	5
Nov-06	2264 ± 156	5	1826 ± 364	5
Dec-06	2205 ±365	6	1662 ± 229	5
Jan-07	2115 ± 346	6	1104 ± 185	6
Feb-07	1880 ± 469	6	1416 ± 425	6
May-07	2415 ± 646	6	1953 ± 280	6
Jun-07	2331 ± 358	4	1962 ± 432	5
Jul-07	2368 ± 277	5	1324 ± 112	2
Aug-07	1823 ± 541	4	1480 ± 259	6
Sep-07	1932 ± 471	6	1602 ± 161	6
Overall	**2168 ± 466**	**65**	**1666 ± 416**	**62**

Stepwise linear regression (SLR) analysis was used to determine variables that most influence daily path length. Although flowers and pith accounted for about 8% of feeding records on average, the ranging data throughout the study period showed that an increase in daily flower and pith consumption resulted in a shorter daily path length (DPL) for the edge group (SLR: $R^2 = 0.253$, $F_{2, 58} = 9.8$, $p \leq 0.0001$) (Figure 9). The percentage of feeding records on pith was sometimes important (*ca* 20%) for the l'Hoest's monkeys of the edge group.

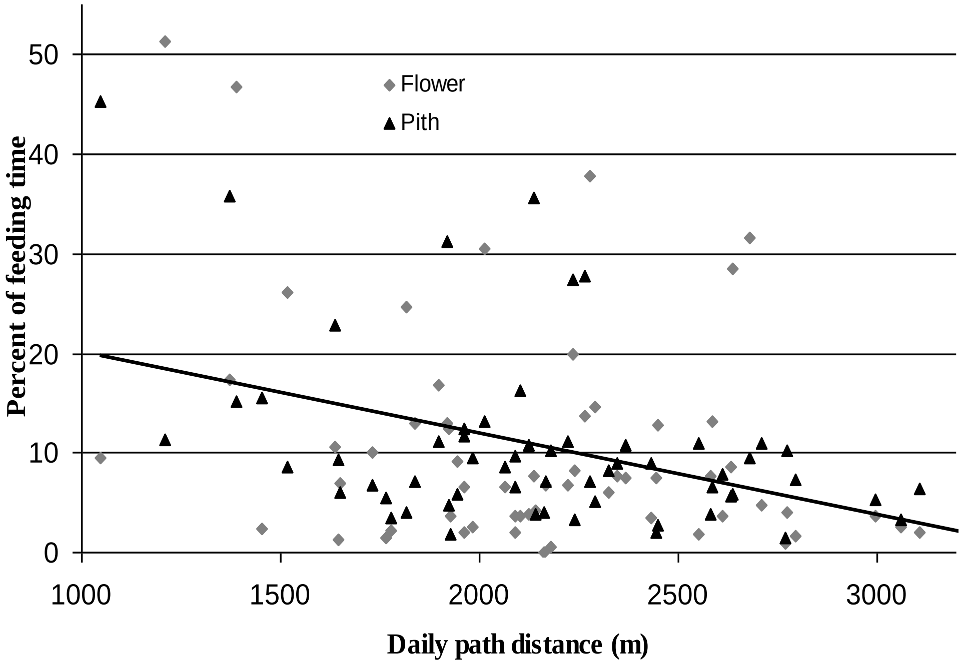

Figure 9. Relationship between daily path lengths and daily feeding rates on flowers and pith by the edge group in the Bwindi forest (both flowers and pith have relatively similar trend lines).

However, fruits, invertebrates, and other food items did not seem to influence the DPL of the edge group. For the first 6 months (July - December 2006), when a large plantation of *Eucalyptus* was being cleared adjacent to the edge group's home range (Figure 10), there was no significant relationship between the DPL and the proportion of feeding records on pith and mature leaves for the edge group. However, between January and September 2007, when the edge group was regularly foraging in the valleys cleared of *Eucalyptus* within the forest (Figure 10), DPL was shorter when more time was spent feeding on a mixture of pith and mature leaves of mainly mint species (*Plectranthus*) and ironweed (*Vernonia*), species that became abundant in the clearing (SLR: $R^2 = 0.315$, $F_{2, 33} = 7.596$, $p \leq 0.005$) (The relationship trend between feeding time on mature leaves (%)

and DPL (m) was also similar to that of flowers in Figure 9). However, feeding on mature leaves represented less than 1% of the total feeding records in the edge group.

Figure 10. Photo of a large area cleared of *Eucalyptus* tree species inside the boundaries of Bwindi forest.

The DPL was not significantly influenced by crop-raiding over the first six months before the edge group had expanded its home range into the area cleared of *Eucalyptus* and over the 13 months of the study as a whole. However, from January to September 2007, when the group began using the area cleared of *Eucalyptus*, the DPLs of the edge group were significantly greater, mainly because of the days when the edge group raided crops outside the park (SLR: $R^2 = 0.130$, $F_{1, 34} = 5.071$, $p \leq 0.05$). On the other hand, the interior group travelled significantly longer daily paths when they fed more on seeds, and shorter daily paths when feeding more on new leaves (SLR: $R^2 = 0.218$, $F_{2, 62} = 8.641$, $p \leq 0.001$, Figure 11).

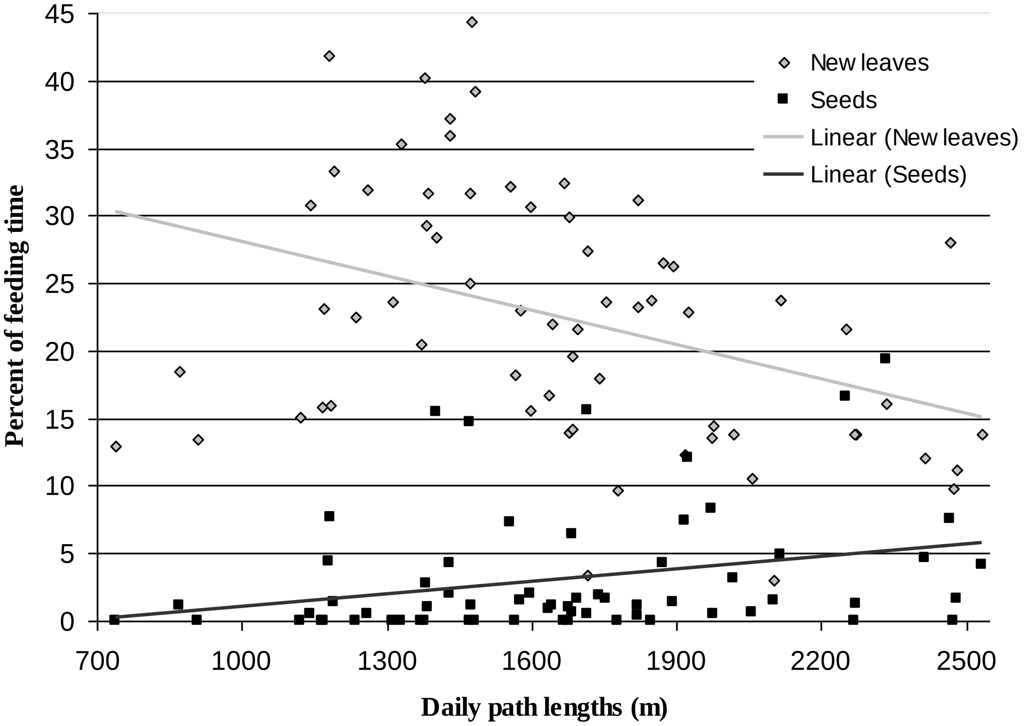

Figure 11. Relationship between daily path lengths and feeding rates on seeds and new leaves by interior group of l'Hoest's monkeys in the Bwindi forest.

Discussion

Edge effects on vegetation and habitat structure

I found some differences in vegetation abundance and distribution from the edge to the interior within the monkeys' homes ranges, although there were no clear patterns along this edge to interior gradient. There was no difference in species dominance following an edge-interior gradient, likely because of the history of the site, including management practices, time since cessation of exploitation, and current site conservation conditions (Schmidt, 2005). Logging appears to have influenced almost the whole park but most intensively up to 6km from the forest edge (Butynski, 1984), and that is probably why there is relatively little variation in tree size classes throughout the park.

However, the canopy cover was greater along the edge than in the interior of the forest in the study site. Furthermore, the density of understory vegetation was higher along the edge of Bwindi. Open interior gaps and edge forests are both generally believed to have a higher species density and richness than interior forest (Rodrigues, 1998).

Aubréville (1938) claimed that certain tropical forests can be defined as a mosaic of former gaps, and this is likely the case for the Bwindi forest, which is composed of a mosaic of permanent and newly created forest gaps. In this study, the composition of understory vegetation in Bwindi was relatively similar from the edge to the interior, indicating that the whole study area may be considered secondary forest in an early successional, recovery stage.

Edge effects and the feeding ecology of l'Hoest's monkeys in Bwindi

There was a remarkable similarity in the diet composition of the edge and interior groups, with no consistent differences in overall feeding records, and this is expected given the lack of clear vegetation differences from the edge to the interior. Nevertheless, the edge group spent more time feeding on "other" food items, including tree bark, gum, animal matters, roots, and crops, than the interior group. The edge group also fed on more food types than the interior group, and slight differences in mean activity records were detected between the groups. Crop raiding was an exclusive activity of the edge group. There were no significant differences in mean monthly consumption of leaves, flowers, fruits, pith, seeds, and invertebrates between edge and interior groups. High dietary overlaps between different subpopulations or groups of the same species have been reported in many other forest *Cercopithecus* monkeys across Africa (Gautier-Hion, 1980; Cords, 1986; Plumptre & Reynolds, 1994; Gathua, 2000). However, in the Kibale forest, Uganda, pronounced differences in habitat characteristics and accompanying diet composition differences were found in groups of *Cercopithecus mitis* located 10 km apart (Butynski, 1990). Chapman et al. (2002a) found that dietary variability was larger among groups of red colobus (*Procolobus badius*) that were far apart than between neighboring groups. Other studies have demonstrated that primate groups living on the edges of forest fragments have diets different from interior or continuous forest groups (Lee 1997; Tutin 1999).

Many factors can explain the general similarity in diets between the two groups in this study. The dietary similarities between the two groups probably reflect low differences in vegetation composition in both home ranges (see Lehman, 2004). The fact that the whole study area in the Bwindi forest was extensively logged 16 years ago suggests that the study area, including edge and interior forest, is composed largely of regenerating secondary forest. Such intense degradation may have created an almost homogeneous habitat from which a clear distinction between edge and interior forests is difficult to make (Heske, 1995). In addition, the fact that the home ranges of both groups were only about 300 m apart could explain the resemblance in their diet.

Overall, the diet of l'Hoest's monkeys in the Bwindi forest was comparable to that of a group studied by Kaplin (2001) in Nyungwe National Park, Rwanda. L'Hoest's monkeys in Bwindi and Nyungwe spent 32% and 35%, respectively, of their time feeding on terrestrial herbaceous vegetation (THV), and proportions of fruits and seeds in their diets were also similar (Kaplin and Moermond, 2000; this study). However, studies of l'Hoest's monkeys in the Kalinzu forest, Uganda (Tashiro, 2005; Tolo et al., 2007) reported that this species fed mainly on insects (up to 66% of the total feeding time), while in Bwindi and Nyungwe forests l’Hoest’s monkeys spent about 10% of their time feeding on invertebrates. Differences in invertebrate consumption by l’Hoest’s monkeys in these forests could be explained by differences in altitude, habitat characteristics, and the duration of research projects. Duration of the studies may be a factor: the research projects in Kalinzu, Nyungwe, and Bwindi were conducted for three, ten, and 13 months respectively. Higher invertebrate species richness has been detected at lower altitudes, diminishing at higher altitudes (Kohlmann et al., 2007). In the montane forests of Nyungwe and Bwindi, the studies were conducted from 2100 m to 2700 m (Kaplin, 2001) and from 1900 m to 2400 m, respectively. Studies on l’Hoest’s monkeys in the medium altitude Kalinzu forest were conducted between 1200 m and 1500 m (Tashiro, 2005; Tolo et al., 2007).

My findings highlight the important role of native vegetation in the diet of the l’Hoest’s monkeys when they forage outside the park. Elsewhere, edge groups of primates (e.g. in India, Singh et al., 2001) were reported to include more food items from a large variety of non-native, crop and pioneer plants in their diet. In Bwindi, although l’Hoest’s monkeys were attracted to local subsistence crops (e.g. maize, sorghum, beans, and potatoes) up to over 500 m outside the forest edge, they fed more frequently on native terrestrial herbaceous plant species that were abundant in fallows just outside the park (±100 m) than on exotic plants.

Edge and interior group home ranges

In this study, the home range of the edge group was larger than that of the interior group. Home ranges serve as the most fundamental descriptor of wildlife space-use and an important variable of ecological analyses (Downs & Horner, 2008). Home ranges are influenced by habitat characteristics as well as the seasonal availability of food resources (Li et al. 2000; Passamani & Rylands, 2000; Gathua, 2000). The differences I found in home range size may be related to several factors.

Efficiency in exploitation of clumped or sparsely distributed food resources such as fruits or gums may explain larger home ranges (Butynski 1990; Passamani and Rylands 2000). In October 2006 of this study, the proportion of time spent by the interior group feeding on fruit and seed was greater than the annual average, which might have been one of the reasons why the October home range area of the interior group was greater than that of the edge group. According to Janson and Goldsmith (1995), relationships between food types and home range sizes of folivorous primates may not be significant since leaves are abundant and more widespread than fruits. In this study, I observed that leaf resources could become limited to lower wet valleys during the dry season, when annual and perennial vegetation desiccated in forest clearings. Such distribution appears to have influenced the movement of l'Hoest's monkeys, who moved parallel to streams and valleys during the dry season, covering a smaller home range.

Crop raiding also had a significant influence on home range size. While crop raiding, the edge group expanded its home range outside the park. Chhangani & Mohnot (2006) found that agricultural crops were responsible for an increase in langur (*Semnopithecus entellus*) home range sizes, particularly because they were found in more open habitats. In forested habitats, primate groups travel less and occupy a smaller home range as long as food resources are abundant (Boonratana, 2000). Interestingly, when l'Hoest's monkeys entered sorghum and maize fields, they had even larger home ranges because they could travel farther inside these fields because of the cover of these tall crops, which prevented guards from spotting and chasing them. Bean fields did not offer this kind of cover to the monkeys. Disturbances associated with the edge may also have influenced home range size. The edge group was constantly on the move because of the presence of noise and attacks from local villagers and their dogs. As Li et al. (2000) pointed out, such disturbances contribute to an increase in home range area for edge groups.

Differences in home range sizes can also be attributed to differences in group size. According to Janson and Goldsmith (1995), home range size increases with group size. The edge group had twice the number of individuals as the interior group. Janson and Goldsmith (1995) have argued that members of a large group may incur additional foraging and ranging costs compared with smaller groups. Each member of a large group reduces available resources for others. To overcome such an effect on foraging efficiency, large groups must travel farther and have larger home ranges in order to satisfy their food intake (van Schaik et al., 1983).

For a territorial species such as l'Hoest's monkey (Gautier-Hion et al., 1999), home range size may also be influenced by how the group is compressed by neighboring conspecific groups. The edge group had the advantage of extending its territory beyond the park boundaries by 12%, where no other l'Hoest's groups existed. Similarly, Passamani and Rylands (2000) speculated that the absence of contact with neighboring groups may have contributed to the increase in home range size of Geoffroy's marmoset (*Callithrix geoffroyi*) in South-Eastern Brazil. More research is needed to understand the influence of forest edge and matrix type on home range size.

The influence of food and forest edge on daily path length (DPL)

L'Hoest's monkeys travelled longer daily path lengths (DPL) when feeding on fruits, seeds, invertebrates, or crops, but shortened daily paths when they spent more time feeding on flowers, pith and leaves. A similar finding was reported by Chhangani and Mohnot (2006) in forest langurs (*Semnopithecus entellus*) that travelled longer daily paths when the groups ate more fruits but travelled less when feeding more on leaves. During the fruiting season at Bwindi, monkeys travelled frequently among remote individual trees of species such as *Prunus africana*, *Chrysophylum albidium*, and *Ficus* spp. Conversely, because herbs are abundant and widespread in the Bwindi forest (Nkurunungi, 2003), l'Hoest's monkeys traveled less when feeding on leaves, pith and flowers of terrestrial herbaceous vegetation. The interior group travelled longer distances when feeding on invertebrates, which may be less abundant in the interior forest than on the forest edge (Lee, 1997; Tutin, 1999). However the movement of primate species and other animals cannot be fully explained by simple identification and mapping of the distribution of the species they feed on. Nutritional composition in terms of value and variations between plant species and other items eaten and also the nutritional needs of a animal species should be taken into account in documenting the driving motives of movements of primate and other animal species (Chapman et al., 2002b; Chapman et al., 2003).

Daily path lengths were generally longer in the edge group than the interior group. This difference may be explained by the variables that also influence home range size, specifically foraging efficiency as well as degree of disturbance to the monkeys. Another explanation is that larger groups must travel farther to obtain adequate food intake

(Janson & Goldsmith, 1995; Chapman et al., 2002b). However, not all studies of primates have supported the assumption that large groups should travel longer distances (Stevenson & Castellanos, 2000; Janson & Boinski, 1992; Altmann, 1974). In this study, although the edge group was twice the size of the interior group and the mean monthly daily path lengths were usually greater than those of the interior group, it was only during crop raiding and periods of disturbances that daily path lengths increased considerably in the edge group. Crops such as sorghum and maize could camouflage and attract l'Hoest's monkeys farther away from the park. Therefore, the daily path lengths of l'Hoest's monkeys in the dry season when this crop was available were longer than in the wet season for the edge group, but the daily path length was rarely double that of the interior group.

According to optimal foraging theory, animals have to balance the benefits or net energy gained with costs (or constraints) associated with a particular food item (Tyler & Calow, 1985). For example, when high-quality and preferred food items such as local crops become seasonally available, animal travel distances will increase to obtain these foods (Bennett, 1986; Baker, 2004). Animals will expend a lot of energy to reach and consume crops because the rewards are high. However, crop raiding by l'Hoest's monkeys in Bwindi angers local people, who guard their farms and chase monkeys away. L'Hoest's monkeys who attempt crop raiding are thus constantly on the move, a costly activity that may affect the fitness, reproduction and survival rates of individuals (see Bercovitch & Strum, 1993 for baboons). Nevertheless, l'Hoest's monkeys have shown some flexibility in dietary selection and have the ability to change their diet according to the availability, quality, and accessibility of food (Chapman et al., 2002b).

CONCLUSION

The edge and interior groups of l’Hoest’s monkeys were characterized by a striking similarity in diet composition. However, edge effects on habitat structure, vegetation distribution, food availability and the intensity of disturbances in Bwindi Impenetrable National Park in Uganda influenced the behavior of the species at the park boundary. There was a correlation between the abundance of food species and the amount of time l’Hoest’s monkeys spent feeding on these species along the forest boundary, while there was no correlation between plant food abundance and feeding time in the interior group; the animals in the interior group fed on different items regardless of their abundance. The edge group had a larger home range than the interior group. Because of using areas outside the park specifically for feeding on non-native vegetation and crops, l’Hoest’s monkeys increased their home range by expanding their territory into farmlands. However, foraging in these edge habitats and in the surrounding matrix, especially in open agricultural fields, was associated with a deacrease in daily path lengths due to easy access to crops and to native vegetation in fallows. Overall however, l’Hoest’s monkeys are likely expending more energy on the forest edge compared with groups in the interior forest to obtain food and avoid risks, but such energy is probably paid off by feeding on crops and other exotic species of relatively higher nutritional value.

LITERATURE CITED

Aubréville A. 1938. *La forêt coloniale – Les forêts de l'Afrique Occidentale Française*. Société d'Éditions Géographiques, Maritimes et Coloniales. Paris.

Altmann S.A. 1974. Baboons, space, time, and energy. *American Zoologist* 14: 221-248.

Andama E. 2007. *Invasive potential of Mauritius thorn (Cesalpinia decapetala) (Roth) Alston and its use to deter crop raiding by wild animals around Bwindi Impenetrable National Park, Uganda*. Dissertation. Makerere University.

Babaasa D., Eliu G., Kasangaki A., Bitariho R. & A. McNeilage. 2004. Gap characteristics and regeneration in Bwindi Impenetrable National Park, Uganda. *African Journal of Ecology* 42: 217-224.

Baker J. 2004. *Evaluating conservation policy: integrated conservation and development in Bwindi Impenetrable National Park, Uganda*. Dissertation. University of Kent. UK.

Bennett E. L. 1986. Environmental correlates of ranging behaviour in the banded langur, *Presbytis melalophos. Folia Primatologica* 47: 26-38.

Bercovitch F.B. & C. Strum. 1993. Dominance rank, resource availability, and reproductive maturation in female savanna baboons. *Behavioral Ecology and Sociobiology* 33: 313-318.

Bibby C.J., M.J. Collias, C.H. Heath, T.H. Timboden, A.J. Jonshton, J.A. Stattersfield & S.J. Thirgood. 1992. *Putting biodiversity on the map: Priority areas for global conservation.* International Council for Bird Preservation. Cambridge. UK. Pp. 193-204.

Bitariho R., McNeilage A., Babaasa D. & R. Barigyra. 2006. Plant harvest impacts and sustainability in Bwindi Impenetrable National Park, S.W. Uganda. *African Journal of Ecology* 44: 14-21.

Boonratana R. 2000. Ranging behavior of Proboscis monkeys (*Nadalis larvatus*) in the Lower Kinabatangan, Northern Borneo. *International Journal of Primatology* 21: 497-518.

Brokaw N.V.L. 1985. *Treefals, regrowth and community structure in tropical forests*. In Pickett S.T.A & P.S. White. *The ecology of natural disturbance and patch dynamics*. Academic Press. London.

Butynski T.M. 1990. Comparative ecology of Blue monkeys (*Cercopithecus mitis*) in high- and low-density subpopulations. *Ecological Monographs* 60: 1-26.

Butynski, T. 1984. *Ecological survey of the Impenetrable (Bwindi) Forest, Uganda, and recommendations for its conservation and management*. New York Zoological Society. New York.

Chapman C.A., L.J. Chapman & T.R. Gillespie. 2002a. Scale issues in the study of primate foraging: Red colobus of Kibale National Park. *American Journal of Physical Anthropology* 117: 349-363.

Chapman, A.C., J.L. Chapman, M. Cords, M.J. Gathua, A. Gautier-Hion, E.J. Lambert, K. Rode, E.G. Tutin & L.J.T. White. 2002b *Variations in the Diets of Cercopithecus Species: Differences within Forests, among Forests, and across Species*. In Glenn M.E. and M. Cords (Eds.). *The Guenons: Diversity and Adaptation in African Monkeys*. Kluwer Academic ⁄ Plenum Publishers. New York.

Chapman C.A., L.J. Chapman, K.D. Rode, E.M. Hauck & L.R. McDowell. 2003. Variation in the nutritional value of primate foods: among trees, time periods, and areas. *International Journal of Primatology* 24: 317-333.

Chhangani A.K. & S.M. Mohnot. 2006. Ranging behaviour of Hanuman Langurs (*Semnopithecus entellus)* in three different habitats. *Primate Conservation* 21: 171-177.

Coley P.D. & J.A. Barone. 1996. Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics* 27: 305-335.

Cords M. 1984. Mating patterns and social structure in redtail monkeys (*Cercopithecus ascanius*). *Zeitschrift fur Tierpsychologie* 64: 313-329.

Cords M. 1986. Interspecific and intraspecific variation in diet of two forest guenons, *Cercopithecus ascanius* and *C. mitis. Journal of Animal Ecology* 55: 811-827.

Cowlishaw G. 1998. The role of vigilance in the survival and reproductive strategies of desert baboons. *Behaviour* 135: 4310452.

Denyer K, B. Burns & J. Ogden. 2006. Buffering of native forest edge microclimate by adjoining tree plantations. *Austral Ecology* 31**:** 478–489.

Downs J.A. & M.W. Horner. 2008. Effects of point pattern shape on home-range estimates. *Journal of Wildlife Management* 72: 1813-1818.

Dunbar, R. I. M. 1988. *Primate Social Systems: Studies in Behavioural Adaptation*. Croom Helm. London.

Enstam K.L. 2002. *Behavioral ecology of perceived risk of predation in sympatric Patas (Erythocebus patas) and Vervet (Cercopithecus aethiops) monkeys in Laikipia, Kenya*. Dissertation. University of California. Davis.

FAO. 1993. *Summary of the final report of the forest resource assessment 1990 for the tropical world*. FAO. Rome.

Ganas J., M.M. Robbins, J.B. Nkurunungi, B.A. Kaplin & A. McNeilage. 2004. Dietary Variability of Mountain Gorillas in Bwindi Impenetrable National Park, Uganda. *International Journal of Primatology* 25: 1043-1074.

Gathua J.M. 2000. *Intraspecific variation in foraging patterns of redtail monkeys (Cercopithecus ascanius) in the Kakamega Forest, Kenya*. Dissertation. Columbia University.

Gautier-Hion A. 1980. Seasonal variations of diet related to species and sex in a community of *Cercopithecus* monkeys. *Journal of Animal Ecology* 49: 237-269.

Gautier-Hion A., M. Colyn & J.P. Gautier. 1999. *Histoire Naturelle des Primates d'Afrique Centrale*. ECOFAC. Libreville. Gabon.

Gillespie T.R. & C.A. Chapman. 2001. Determinants of group size in the red colobus monkey *(Procolobus badius):* an evaluation of the generality of the ecological constraints model. *Behavioral Ecology and Sociobiology* 50: 329–338.

Hamilton A.C. 1988. *Guenon evolution and forest history*. In: Gautier-Hion A., F. Bourlière, J.-P. Gautier & J. Kingdon (Eds.). *A Primate radiation: Evolutionary biology of the African Guenons.* Cambridge University Press. Cambridge. UK. Pp. 13-34.

Harris, L. D. 1984. *The fragmented forest: island biogeography theory and the preservation of biotic diversity*. University of Chicago Press. Chicago.

Heske E.J. 1995. Mammalian abundances on forest-farm edges versus forest interiors in Southern Illinois: Is there an edge effect? *Journal of Mammalogy* 76: 562-568.

Howard P.C. 1991. *Nature conservation in Uganda's tropical forest reserves*. IUCN. Gland. Switzerland.

Janson C.H. & S. Boinski. 1992. Morphological and behavioral adaptations for foraging in generalist primates: The case of the cebines. *American Journal of Physical Anthropology* 88: 483-498.

Janson C.H. & M.L. Goldsmith. 1995. Predicting group size in primates: foraging costs and predation risks. *Behavioral Ecology* 6: 326-336.

Jenrich R.I. & F.B. Turner. 1969. Measurement of non-circular home range. *Journal of Theoretical Biology* 22: 227-237.

Kaplin B.A. & T.C. Moermond. 2000. Foraging of the Mountain Monkey (*Cercopithecus lhoesti*): Implications for its evolutionary history and use of disturbed forest. *American Journal of Primatology* 50: 227-246.

Kaplin B.A. 2001. Ranging behavior of two species of guenons (*Cercopithecus lhoesti* and *C. mitis doggetti*) in Nyungwe Forest Reserve, Rwanda. *International Journal of Primatology* 22: 521-548.

Kenward R.E. 2001. *A manual for wildlife radio tagging*. Academic Press. San Diego. USA.

Kohlmann B., A. Solis, O. Elle, X. Soto & R. Russo. 2007. Biodiversity, conservation, and hotspot atlas of Costa Rica: a dung beetle perspective (Coleoptera: Scarabaeidae: Scarabaeinae). *Zootaxa* 1457: 1-34.

Lande R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* 76: 5-13.

Laurance W. F., T. E. Lovejoy, H. L. Vasconcelos, E. M. Bruna, R. K. Didham, P. C. Stouffer, C. Gascon, R. O. Bierregaard, S. L. Laurance & E. Sampaio. 2002. Ecosystem decay of Amazonian forest fragments: A 22-year investigation. *Conservation Biology* 16: 605-618.

Laurance, W. F. & R. O. Bierregaard Jr. (Eds.) 1997. Tropical forest remnants. Ecology, management, and conservation of fragmented communities. University of Chicago Press. Chicago.

Lee R. J. 1997. *The Impact of Hunting and Habitat Disturbance on the Population Dynamics and Behavioral Ecology of the Crested Black Macaque* (*Macaca nigra*). Dissertation. University of Oregon. Eugene. USA.

Lehman S.M. 2004. Biogeography of the primates of Guyana: effects of habitat use and diet on geographic distribution. *International Journal of Primatology* 25: 1225-1242.

Lehman S. M., A. Rajaonson, & S. Day. 2006a. Lemur responses to edge effects in the Vohibola III Classified Forest, Madagascar. *American Journal of Primatology* 68: 293-299.

Lehman S. M., A. Rajoanson, & S. Day. 2006b. Edge effects and their influence on lemur distribution and density in southeast Madagascar. *American Journal of Physical Anthropology* 129: 232-241.

Lehman S.M., A. Rajaonson & S. Day. 2006c. Edge effects on the density of *Cheirogaleus major. International Journal of Primatology* 27: 1569-1588.

Li B., C. Chen, W. Ji & B. Ren. 2000. Seasonal home range changes of the Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) in the Qinling Mountains of China. *Folia Primatologica* 71: 375-386.

Lidicker W.Z. 1999. Responses of mammals to habitat edges: an overview. *Landscape Ecology* 14: 333-343.

Martin P. & P. Bateson. 1986. *Measuring behaviour: an introductory guide*. Cambridge University Press. Cambridge. UK.

McNeilage A., A.J. Plumptre, A. Brock-Doyle & A. Vedder. 2001. Bwindi Impenetrable National Park, Uganda: Gorilla census 1997. *Oryx* 35: 39-47.

Menon S. & F.E. Poirier. 1996. Lion-tailed macaques *(Macaca silenus)* in a disturbed forest fragment: activity patterns and time budget. *International Journal of Primatology* 17: 969-985.

Merriam G. & J. Wegner. 1992. Local *extinctions, habitat fragmentation and ecotones*. In. Hansen A.J. & F. Di Castri (Eds.). *landscape boundaries: Consequences for biotic diversity and ecological flows.* Springer-Verlag. New York. Pp. 423-438.

Nkurunungi J.B. 2003. *The availability and distribution of fruit and non-fruit plant resources in Bwindi: Their influence on gorilla habitat use and food choice*. Dissertation. Makerere University.

Nkurunungi J.B., J. Ganas, M.M. Robbins & C.B. Stanford. 2004. A comparison of two mountain gorilla habitats in Bwindi Impenetrable National Park, Uganda. *African Journal of Ecology* 42: 289-297.

Olupot, W. 2004. *Boundary edge effects in Bwindi Impenetrable National Park*. Institute of Tropical Forest Conservation. Uganda. Pp 127-186.

Passamani M. & A.B. Rylands. 2000. Home range of a Geoffroy's marmoset group, *callithrix geoffroyi* (Primates, Callitrichidae) in South-eastern Brazil. *Revista Brasileira de Biologia* 60: 275–281.

Pimm, S.L. & P. Raven. 2000. Extinction by numbers. *Nature* 403: 843-845.

Plumptre A.J. & V. Reynolds. 1994. The effect of selective logging on the primate populations in the Budongo Forest Reserve, Uganda. *Journal of Applied Ecology* 31: 631-641.

Raboy B.E. & J.M. Dietz. 2004. Diet, foraging and use of space in wild Golden-headed lion tamarins. *American Journal of Primatology* 63: 1-15.

Richard A.F., S.J. Goldstein & R.E. Dewar. 1989. Weed Macaques: The evolutionary implications of Macaques feeding ecology. *International Journal of Primatology* 10: 569-594.

Rodrigues E. 1998. *Edge effects on the regeneration of forest fragments in south Brazil*. Dissertation. Harvard Univesity. USA.

Schmidt W. 2005. Herb layer species as indicators of biodiversity of managed and unmanaged beech forests. *Forest Snow and Landscape Research* 79: 111-125.

Seaman D.E. & R.A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* 77: 2075-2085.

Siex K. 2003. *Effects of population compression on the demography, ecology, and behavior of Zanzibar red colobus monkeys (Procolobus kirkii*). Dissertation. Duke University. USA.

Singh M., H.N. Kumara, M.A. Kumar & A.K. Sharma. 2001. Behavioural responses of Lion-tailed macaques (*Macaca silenus*) to a changing habitat in a tropical rain forest fragment in the western Ghats, India. *Folia Primatologica* 72: 278-291.

Sokal R.R. & F.J. Rohl. 1981. *Biometry*. Freeman and Company. San Fransisco. USA.

Stevenson P.R. & M.C. Castellanos. 2000. Feeding rates and daily path range of the Colombian wooly monkeys as evidence for between- and within-group competition. *Folia Primatologica* 71: 399-408.

Stevens S.M. & T.P. Husband. 1997. The influence of edge on small mammals: evidence from Brazilian Atlantic forest fragments. *Biological Conservation* 85: 1-8.

Tashiro Y. 2005. Frequent insectivory by two guenons (*Cercopithecus lhoesti*) and *Cercopithecus mitis*) in the Kalinzu Forest, Uganda. *Primates* 47: 170-173.

Terborgh J. 1992. Maintenance of diversity in tropical forests. *Biotropica* 24: 283-292.

Tolo C.U., J. Baranga & G. Kagoro-Rugunda. 2008. Dietary selection of l'Hoest monkeys in Kalinzu forest reserve, southwestern Uganda. *African Journal of Ecology* 46: 149-157.

Tukahirwa, E.M. & D.E. Pomeroy. 1993. *Bwindi Impenetrable Forest: baseline study report*. Makerere University Institute of Environment and Natural Resources. Kampala. Uganda.

Tutin, C. E. G. 1999. Fragmented living: Behavioral ecology of primates in a forest fragment in the Lope Reserve, Gabon. *Primates* 40: 249-265.

Tyler P. & P. Calow. 1985. *Fish energetics: new perspectives*. Croom Helm Ltd. Kent. UK.

van Schaik C.P., M.A. van Norwijk, R.J. de Boer & I. den Tonkelaar. 1983. The effect of group size on time budgets and social behaviour in wild long-tailed macaques (*Macaca fascicularis*). *Behavioral Ecology and Sociobiology* 13: 173-181.

Whitmore, T.C. 1997. *Tropical forest disturbance, disappearance, and species loss*. In: Laurance W.F. & R.O. Bierregaard Jr (Eds.). *Tropical forest remnants: ecology, management, and conservation of fragmented communities*. Cambridge University. Department of Geography. Downing Place. Cambridge. UK.

Wong S.N.P. & P. Sicotte. 2007. Activity budget and ranging patterns of *Colobus vellorosus* in forest fragments in Central Ghana. *Folia Primatologica* 78: 245-254.

Woodroffe R. & J.R. Ginsberg. 1998. Edge effects and extinction of populations inside protected areas. *Science* 280: 2126-2128.

Zanette L.P. Doyle & S.M. Tremont. 2000. Food strategies in small fragments: evidence from an area-sensitive passerine. *Ecology* 81: 1654-1666.

APPENDICES

Appendix 1. Herb and understory plant species density (per m^2) in the Bwindi forest.

Species name	Growth type	15m	165m	315m	1000m	1700m
Achyranthes aspera	Herb	3.8	2.1	0.7	0.6	0.7
Adenia sp.	Herb	0.1	0.4		0.1	
Agauria salicifolia	Tree		0.3			
Alangium chinense	Tree	0.2	0.1			
Albizia gummifera	Tree	1	0.1	0.2		
Alchornea hirtella	Vine					0.1
Allophyllum abyssinica	Tree	1.2	3	3.8	0.7	0.5
Allophyllum macrobotrys	Tree				0.3	0.6
Asplenium sp.	Fern	9.4	17.1	34	9.7	2.7
Basella alba	Herb		0.3			0.7
Bridelia micrantha	Tree	0.1	2.4	0.7		
Brillantasia nitens	Herb					1.5
Carica papaya	Tree		0.1	0		
Cassipourea sp.	Tree				0.3	
Celosia stelmaninia	Herb			0.3		
Chrysophyllum albidum	Tree			0	0.1	
Cissus (arguta) oliveri	Herb	0.4		0.4		0.1
Clausena anisata	Tree		0.1	0.5		
Clerodendrum sp.	Vine	0.5	0.2	0.6	0.5	0.7
Clutia abyssinica	Shrub	1.3	0.3		0.5	
Coccinia grandis	Herb		0.5			
Coccinia mildbraedii	Herb				0.1	
Commelina sp.	Herb	4.2	0.5	0.5	0.8	0.6
Connarus longistipitatus	Shrub	0	0.1	0.1	0.1	0
Crassocephalum rubens	Herb	2.5	1	1.3	0.6	0.8
Culcasia falcifolia	Shrub	1.4		1.6		
Cyathea manniana	Fern	0	0.1	0.1	0.2	1
Cyperus sp.	Herb	0.1	0	0.1		
Cyphostemma bambuseti	Herb		0.1		0.3	
Cyphostemma sp.	Herb					0.4
Desmodium rependum	Herb		1.2	1.5	0.2	0.6
Dicliptera laxata	Herb					2.1
Dolichos sp.	Herb	0.1				
Dombeya goetzenii	Tree					0.3
Draceana laxissima	Vine	0.4			0.3	0.1
Droguetia iners	Herb	0.3	0.8			
Drymaria cordata	Herb	5.8	0.7	0.2	0.5	4.4
Embelia schimperi	Herb			0.1		
Phyllanthus fischeri	Herb	2.3	0.9	1.1		
Erythrococca trichogyne	Shrub	0	0.6	0.4		
Galiniera coffeoides	Tree	0.4		0.4		
Geranium arabicum	Herb					0.2
Gloriosa superba	Herb	0.1		0.2		

Species name	**Growth type**	**15m**	**165m**	**315m**	**1000m**	**1700m**
Ilex mitis	Tree			0.1		
Impatiens sp.	Herb			0.5	0.1	0.3
Ipomea sp.	Herb	2.3	1.7	1.3	0.2	4.4
Jasminum eminii	Herb	0.5				
Justicia sp.	Herb	0.1				
Justicia striata	Herb	4.1	1.7	6.5	3.2	7
Kalanchoe densiflora	Herb	1.7			0.1	
Laportea aestuans	Herb					0.3
Macaranga kilimandscharia	Tree	0.1		0.3		0.1
Maesa lanceolata	Tree		0.1			0.7
Maytenus senegalensis	Shrub		0.1	0.4		
Mikania cordata	Vine					0.1
Mimulopsis solmsii	Vine	2.1	3.8	2.3	14.5	15
Momordica charantia	Herb	0.1				0.3
Momordica pteridium	Herb		0.1	0.1	0.1	2.5
Monopsis stellarioides	Herb	0.8	0.1	1.7	0.2	0.6
Myrianthus holstii	Tree			0.1		
Neoboutonia macrocalyx	Tree				0.2	0.5
Olinia usambarensis	Tree	0.6				
Orthosiphon australis	Herb	1.9	4	0.6	0.1	1
Kosteletzkya adoensis	Herb				0.1	
Oxyanthus speciosus	Shrub				0.2	
Panicum sp.	Herb	113.3	29.1	8.8	36.3	17.5
Pavetta ternifolia	Shrub	0	0	0.1		
Pavonia urens	Herb	0.1	0.3			
Pentas bussei	Herb	0.1	0.6			
Periploca linearifolia	Herb	0.1				
Phytolacca dodecandra	Herb					0.1
Pilea holstii	Herb	0.1	0.1	0.2		2.9
Piper capense	Herb	0.2	3.5	0.9	0.7	0.1
Pittasporum mannii	Tree		0.1			0.1
Plectranthus albus	Herb	2.8	0.6		0.4	1.4
Plectranthus edulis	Herb	2			1.2	1.6
Plectranthus luteus	Herb	3.5		0.3	4.3	
Podocarpus milanjianus	Tree				0.1	0.8
Polygonum salicifolium	Herb	0.1				
Praquetina sp.	Herb				1.4	
Pristimera graciliflora	Herb	0.7	0.3	0.9	0.8	0.1
Prunus africana	Tree	0.7	22.8	1.9	0.3	0.1
Psychotria kirkii	Shrub	1.9	0.4	0.3	0.6	0.3
Psychotria monii	Tree		0.3	0.1	3.6	1.7
Pteridium sp.	Fern	0.7		0.1	1.4	1.6
Pteris sp.	Fern	0.1	0.1	0.6	0.1	0.2
Pterolobium sp.	Herb	0.3	1	0.5		
Ranunculus multifidus	Herb	0.3				
Rubus sp.	Vine	1.2	0.5	0.2	0.9	1.1
Rumex abyssinicus	Herb	0.1				
Rutidea orientalis	Vine	1.3	0.7	1.4	0.2	
Rytiginia beniensis	Tree	0.1	0.6		0.3	

Species name	**Growth type**	**15m**	**165m**	**315m**	**1000m**	**1700m**
Rytiginia bugwensis	Tree	0.1	0.3			
Rytiginia ruwenzoriansis	Tree		0.3	1.1	1.9	0.1
Salacia leptoclada	Vine					0.1
Securidaca welwitschii	Vine	2.1	0.6		0.6	0.6
Sercostachys scandens	Vine	0.1	0.1	0.3	1.5	1.5
Smilax anceps	Herb	0.1				
Spermacoce princeae	Herb	0.1		1.2		
Stanrogyne alboviolacea	Herb				1.6	
Strombosia scheffreri	Tree				0.2	
Symphonia globulifera	Tree	0.2				
Teclea nobilis	Tree					0.2
Thunbergia alata	Herb			0.1		0.5
Triumfetta green	Herb	0.8	1.8	0	0.8	1.1
Triumfetta sp2.	Vine	1	0.4	1.1	1.2	1.1
Unidentified 1	Shrub	0.1		0.1		
Unidentified 2	Herb	0.1				
Unidentified 3	Herb	0.1			0.1	
Urera sp.	Vine	0.1	0.1	1.2		0.9
Vernonia calongansis	Shrub		0.2			
Vernonia lasiopus	Shrub	0.4	0.2	0.4	0.6	0.2
Xymalos monospora	Tree	0.3	1.1	1.8	0.1	0.1

Appendix 2. Percentage of fruit-feeding observation records devoted to each fruit species for the edge and the interior groups of l'Hoest's monkeys in the Bwindi forest.

	Percentage fruit feeding records	
Plant species	**Edge group**	**Interior group**
Bridelia micrantha	3	0.17
Carica papaya	2.43	0.51
Chrysophylum albidium	0.14	4.05
Clutia abyssinica	0.29	0.17
Coccinia grandis	0.86	0.84
Cyphomandra betacea		0.17
Cyphostemma bambuseti	0.14	
Momordica charantia	0.86	0.17
Momordica pterocarpa	0.43	0.51
Myrianthus holstii	3.29	
Prunus africana	6.87	7.08
Rapannea rhododendroides	0.14	
Ritchiea albersi	0.14	0.67
Rubus sp.	4.58	11.3
Rytiginia ruwenzoriensis	4.58	4.55
Solanum sp.	1.14	1.18
Strombosia scheffleri	0.14	4.55
Symphonia globulifera	0.29	
Syzigium cordatum	0.14	
Syzigium guineense	3.72	3.71
Tabernaemontana holstii	0.14	4.05
Unidentified sp. (Rubiaceae)	0.14	0.67
Xymolos monospora	0.43	0.17
Cassipourea sp.	0.14	4.38
Dombeya goetzenii	0.14	
Dovyalis macrocalyx	1.29	0.34
Dovyalis macrocalyx		0.17
Galiniera coffeoides	12.59	3.88
Hibiscus densiflora	0.29	
Impatiens sp.	0.14	0.84
Lutidia orientalis	2.15	0.84
Maytenus senegalensis	0.14	
Olea capensis		0.34
Olea usambarensis	0.14	1.18
Physiaris peruviana	1	
Piper capense	10.3	3.88
Plectranthus edulis	0.14	
Plectranthus sp	0.14	
Podocarpus milanjianus		3.2
Polyscias fulva	0.43	
Psychotria mahonii	0.86	5.9
Psychotria PE	0.29	
Rytiginia beniensis	2.86	0.17
Rytiginia bugwensis	0.57	0.17
Rytiginia kigeziensis	0.43	0.17

Plant species	**Edge group**	**Interior group**
Selacia elgans	0.14	1.52
Teclea nobilis	0.14	0.17
Thunbergia alata	0.14	
Acacia mearnsii	0.86	
Adenia sp.	0.29	0.34
Alangium chinense	0.14	
Albizia gummifera	0.14	
Alchornea hirtella	0.43	0.34
Allophyllum abyssinica	2.29	5.56
Allophylum macrobotrys	0.43	4.55
Desmodium rependum	0.43	0.17
Embelia schimperi	0.29	
Englina spp.	0.86	0.51
Erretia cymosa	0.29	
Erythrococca trochogyne	5.87	1.52
Ficus sp.	3	5.73
Laportea aestuans	0.14	
Maesa lanceolata	6.72	4.55
Maytenus aethiopica	0.29	0.84
Myrica salicifolia	4.29	0.34
Orchid species	0.72	0.34
Oxyanthus speciosus	0	0.17
Pottasporum manii	0.29	
Pyschotria kirkii	0.57	2.87
Rhys natalensis	1.72	
Trema orientalis	1.29	
Unidentified sp.	0.29	0.51

Appendix 3. Plant, animal matter and other food types recorded in the diet of the edge and interior groups of l'Hoest's monkeys in Bwindi Impenetrable forest (FL = flowers, LV = leaves, FR = fruits, SD = seeds, OT represents roots, tendrills, petioles, gum, animal matters, soil and water).

Species	**Edge group**						**Interior group**					
	FL	**FR**	**LV**	**OT**	**PT**	**SD**	**FL**	**FR**	**LV**	**OT**	**PT**	**SD**
Acacia mearnsii	1.26	0.7	0.04	6.27		55.9						
Achyranthes aspera			0.04									
Adenia gummifera	0.08	0.09	0.04		0.23			0.08				
Aeschynomene sp.	0.08					0.25						
Agauria salicifolia					0.11							
Alangium chinense	0.16	0.02	0.04		0.11							
Albizia gummifera		0.04	0.11	14.9	0.23	0.25				8.299		
Alchornea hiltella	0.24	0.44			1.02			0.08			1.13	
Allophyllum abyssinica	0.39	4.86	0.11	0.14	0.34		0.15	12.8	0.03			
Allophyllum macrobotrys		0.61	0.04		0.23		0.15	8.48	0.06			
Asplenium sp.			4.84	1.81	0.23			0.03	4.27	16.18		
Basela alba			1.86	0.28					2.43	0.415		
Bersama abyssinica								0.05	0.03		0.32	
Bridelia micrantha		2.66	0.07		0.68			0.1				
Caesalpinia sp.				0.7	0.11	5.69						
Carica papaya	0.24	1.05	0.04	4.04	0.23			0.13				
Carpodinus glabra			0.04									
Cassipourea gummifera		0.02	0.07				0.15	5.17	1.75			
Celosia stelmaninia											0.16	
Chrysophyllum albidium		0.02						8.38				
Citrullus colocynthis	0.63	0.02	0.14	0.28			0.15		0.16			
Clausena aniseta			0.04									
Clerodendrum sp.			0.04		2.03		0.15				4.35	
Clutia abyssinica		0.04					0.44	0.03				
Coccinia barteri			0.04						0.03			
Coccinia grandis	1.65	0.26	0.7	0.42	0.34		0.29	0.2	0.52		0.32	
Coccinia mildbraedii		0.02	0.07	0.14	0.23		0.15		0.1		0.32	
Commelina africana			0.18				0.88		0.55		0.97	
Commelina sp.			1.93				0.59	0.03	0.62		0.16	
Crassocephalum rubens	0.08		0.04		7.79						2.1	
Crassocephalum vitellinum	0.08											
Croton macrostachys			0.04									
Cryptolepsis senguinolenta			0.21		0.23							
Culcasia falcifolia		0.02										
Cyathea manniana					0.11				0.03		1.13	
Cyperus renschii	0.08					0	0.74					
Cyphomandra betacea								0.05	0		0.32	

	FL	FR	LV	OT	PT	SD	FL	FR	LV	OT	PT	SD
Cyphostemma bambuseti	0.08	0.02						0.03	0.03			
Desmodium rependum	7.01	0.09	0.74			2.48	0.44	0.03	0.42		0.32	0.35
Dicliptera laxata		0.07							0.03			
Dombeya goetzenii			0.07		0.11			0.03	0.06	0.415	0.16	
Dovyalis macrocalyx	0.08	0.33	0.07		0.11		0.15	0.1				
Draceana laxissima	0.16		0.21						0.1			
Droguetia iners			0.14						0.06			
Drypetes gerrardii									0.03			
Ekebergia capensis		0.02	0.28	0.28					0.03			
Embelia schimperi		0.5	1.19		0.34							
Engelina spp.	1.02	0.24	0.07				0.44	0.08				
Entandrophragma excelsum				0.14								
Erretia cymosa					0.11							
Erythrina abysinica	0.08		0.07	0.14	0.23							
Erythrococca trichogyne	1.34	6	15.9		0.23		0.15	0.63	1.07			
Faurea saligna	0.08	0.02	0.04		0.23							
Ficus sp.		2.51	0.14					9.69				
Galiniera coffeioides	0.39	10.6	0.04		4.4			0.98	0.03		0.16	
Geranium arabicum			0.14		0.34	0.25			0.29		0.32	
Gloriosa superba			0.04									
Govania longispicata			0.04		0.23							
Hibiscus densiflora	0.08	0.07			0.11		1.18					
Ilex mitis			0.04						0.26			
Impatiens sp.	3.07	0.02	0.6		0.34		2.8	0.13	0.94		0.16	
Ipomea sp.	48.5		12.5			5.45	42.6	0.05	19.8			
Jasminum eminii									0.03			
Justicia striata			0.11				4.27		1.68			
Justicia sp.			0.04						1.17			
Lactuca grandiflora			0.04									
Lantana camara		0.02										
Laportea aestuans							0.15		2.69			
Leonotis nepetifolia			0.04		0.11							
Leptaspis zylenica	0.16											
Macaranga kilimandscharica	0.08		0.04	0.28	2.14						0.32	
Maesa lanceolata	3.15	22.4	0.04	0.14			0.15	6.35	0.03	1.245		
Maytenus accuminata		0.04										
Maytenus aethiopica		0.09	0.04		0.45			0.13				
Maytenus senegalensis	0.16	3.51	0.14		1.92			0.03				
Mimulopsis arborescens				0.14	0.23							
Mimulopsis solmsii				0.14				0.03	0.87		0.48	
Momordica charantia	0.47	0.26	1.23					0.03	1.55			
Momordica pterocarpa	1.34	0.13	1.65	2.79			1.03	0.13	2.75	1.66		0.35

	FL	**FR**	**LV**	**OT**	**PT**	**SD**	**FL**	**FR**	**LV**	**OT**	**PT**	**SD**
Monopsis stellarioides	0.08		0.46				0.15		0.97			
Myrianthus holstii	0.08	2.29		0.42	2.26							
Neoboutonia macrocalyx				0.14	0.45				0.26	1.245	34	
Nuxia congesta		0.02										
Olea capensis		0.2	0.84		0.11		3.83	0.08	0.94	1.245		66.8
Olinia usambarensis		0.09	0.04			0.25		0.35				
Orchid species	1.42	0.11	0.39	0.84			1.77	0.05	0.23	0.83		0.35
Orthisiphon australis	0.08		0.04						0.06			
Oxyanthus speciosus								0.05				
Panicum sp.	0.16	0	12.4	0.28		0.74	0.15		0.39			0.69
Pavetta ternifolia	0.08	0	1.26						2.04			
Pavonia urens	1.02	0.02										
Pentas bussei			0.32						0.03			
Pentas parvifolia			0.21									
Periploca linearifolia			0.46									
Physialis peruviana	0.24	0.15										
Piper capensis	0.87	6.56		0.28	2.14			1.68	0.03		1.94	
Piper guineense									0.03			
Pittasporum mannii	0.08	0.13			0.23					0.415		
Plectranthus albus							1.77	0.03				
Plectranthus edulis	0.47	0.02	0.11		0.34	0	8.39		1.65	0.83	5	
Podocarpus milanjianus								1.83	0.06	0	0.16	
Polygonum salicifolium	0.32	0.02						0.03				
Polyscias fulva	4.18	0.15	0.04	20.2						2.905		
Pristimera graciliflora						0.25						
Prunus africana		13		30.8			0.88	13.3		59.34		
Psychotria kirkii	0.47	0.15					3.68	1.36	0.06		0.16	
Psychotria mahonii	12.4	0.37	0.11		0.34		12.7	5.3	0.13			
Psychotria pendiculans		0.07										
Pteridium sp.			16.1	0.14	0.34			0	33.1		1.94	
Rapennea rhododendroides		0.04			0.79			0.03				
Rhus natalensis	0.95	0.44	1.16		3.72							
Ritchiea albersi		0.02	0.21					0.13	0.03			
Rubia cordifolia			0.11						1.13		0.65	
Rubus sp.	0.08	1.24	0.21		9.71		0.15	4.04	0.13	0.415	26	
Rumex abyssinicus					0.11							
Rumex sp.			0.11									
Rumex usambarensis		0	0.11								0.32	
Rutidia orientalis	1.34	1.16	0.25	3.2	1.58		0.44	0.13	0.03		0.16	
Rytiginia beniensis		1.16	1.33		0.34			0.03	0.42			
Rytiginia bugwensis		0.2	0.95	0.14	0.34			0.25	0.36			
Rytiginia kigeziensis		0.13	0.46	0	0.23		3.68	0.1	0.13			
Rytiginia ruwenzoriensis		5.65	0.32	0.14	0.11		2.21	6.05	0.45			
Salacia elgans		0.02	0.04				0.15	0.28	0.03			

	FL	**FR**	**LV**	**OT**	**PT**	**SD**	**FL**	**FR**	**LV**	**OT**	**PT**	**SD**
Salacia leptoclada	0.24	0.02	0.04	0.14	0.11	22.8						
Securida welwitschii	0.08		0.35		24.9				0.03		6.29	
Sercostachys scandens	0.24				0.11				0.16	0.415		
Smilax anceps			0.46		0.45		0.15				0.32	
Solanum anguvu					0.11							
Solanum sp.	0.08	0.28			0.11			0.28			0.65	
Stanrogyne alboviolacea			0.04						0.03			
Streptocarpus caulescens			0.04									
Strombosia scheffleri		0.02						2.33		0.415	0.16	21.5
Symphonia globulifera		0.2										
Syzigium cordatum		0.28										
Syzigium gummifera	0.08	6.17	0.04			0.25		5.72				
Tabernaemontana hostii		0.11						1.26		1.245		
Teclea nobilis		0.57							0.06	1.245		
Thunbergia alata		0.02					0.44		0.55		0.32	
Trema orientalis		0.55										
Triumfetta spp.	0.08		3.16		0.23				3.24		0.16	
Triumfetta spp.	0.47		0.21		0.68		0.44				0.16	
Umbelinia kigeziansis	0.08		1.61									
Unidentified 1								0.1	0.03			
Unidentified 2			0.35	0.14	0.34			0.1	0.26		0.32	
Unidentified 3			0.07				0.15		0.13		0.16	
Unidentified 4	0.16		0.04		0.23		0.29		0.52			
Unidentified 5			0.07									
Unidentified 6	1.1	0.35	1.86	0.28	0.79	0.25	0.44	0.25	1.3	0.83	1.29	1.04
Unidentified climber			0.11					0.23	0.36		0.16	
Unidentified Rubiaceae		0.02	0.07					0.25	0.71			
Urera sp.			6.14		1.92		0.29	0.08	4.95		0.16	
Vernonia auriculifera					0.11							
Vernonia calongansis					9.59						1.61	
Vernonia lasiopus					1.81						0.16	
Vernonia sp.					2.82				0.1		0.81	
Xymolos monospora		0.09	0.32	0.14	4.97		0.15	0.08	0.03	0.415	3.39	
Zehneria minutiflora			0.04									
Species vernacular name												
Ehongwe	0.08		0.04		0.11							
Emboha									0.03		0.16	
Ibihimbabyenkima							0.15					
Ikizimyamuriro									0.03			
Inkizi			0.07									
Inkobakoba								0.03				
Intawutara		0.04										

Food items	**FL**	**FR**	**LV**	**OT**	**PT**	**SD**	**FL**	**FR**	**LV**	**OT**	**PT**	**SD**
Inyongera								0.03				
Itumezi								0.13				
Kaboha									0.19			
Omukanja			0.04		0.11							
Omucasuka	0.08											
Omufumba									0.06		0.16	
Omugabagaba							0.15					
Omukatampiri		0.02										
Omukobakoba								0.15				
Omusekera	0.08											
Omuzigaziga	0.16											
Orukoka							0.29					
Orusharara	0.08											
Local crop species												
Beans			0.42			0.25						
Maize						0.99						
Potato	0.32		0.04	9.75	1.47							
Sorghum						3.96						
Other plant classes												
Lichen				1.48						0.74		
Moss				0.18					0.26			
Mushroom				5.72						7.8		
Invertebrate												
Ants				0.05						0.05		
Bagworm				0.02								
Beatle										0.01		
Butterfly										0.05		
Caterpillar				0.25						0.15		
Grasshopper				0.03						0.03		
Mantis				0.01								
Millipede										0.01		
Spider				0.03						0.03		
Worm				0.48						0.04		
Snail				0.02						0.02		
Moth				0.03						0.07		
Animal matter												
Chameleon				0.03								
Bird chicks										0.02		
Bird eggs				0.02								
Lizard										0.02		
Rats				0.01								
Others												
Water				0.08						0.06		
Soil				0.15						0.27		

CHAPTER 4

FOREST EDGE EFFECTS ON THE BEHAVIORAL ECOLOGY OF THE L'HOEST'S MONKEY (*CERCOPITHECUS LHOESTI*) IN BWINDI IMPENETRABLE NATIONAL PARK, UGANDA

ABSTRACT

Forest edge effects result from changes in physical features of the habitat, predator species or numbers, and prominence of human activities and other disturbances that can have direct or indirect impact on the behavior, ecology, and fitness of forest animal species. I studied how edge-related disturbances influenced the behavioral ecology and survival strategies of the l'Hoest's monkey (*Cercopithecus lhoesti*) in Bwindi Impenetrable National Park in Uganda. I habituated a group of l'Hoest's monkeys located at the edge of the forest and a group towards the forest interior. Using instantaneous scan sampling methods, I recorded activity budgets in each group over 13 months. The behavior of the edge group was remarkably similar to that of the interior group. However, the edge group socialized significantly less compared with the interior group, an activity that could reduce the cohesion in the edge group. In addition, the edge group's daily path lengths and home ranges exceeded those of the interior group mostly due to edge disturbances. During crop raiding, which only the edge group engaged in, the edge group's daily path lengths were shortened, because they spent time being still and observing the surroundings to make sure it was safe to go outside the park. Greater group turnover and higher mortality was observed in the edge group than in the interior group. Eight individuals (22% of the original total edge group members) died in the edge group during my study. Four were victims of human retaliation, 1 was killed by an eagle and three were possibly victims of infanticide committed by new adult males that took over the edge group. In contrast, the interior group lost only two individuals (11%) during the study. Since four l'Hoest's monkeys of the edge group were killed by local farmers, conservationists should invest more resources to mitigate human-wildlife conflicts along park boundaries.

KEY WORDS: L'Hoest's monkeys, edge effects, edge disturbances, behavioral ecology, crop raiding, survival strategies, Bwindi Impenetrable forest.

INTRODUCTION

Forest edge effects result from changes in physical features in the habitat, increases in predator numbers or species, and a predominance of anthropogenic activities that can have direct or indirect impact on the behavior, ecology, and fitness of animal species (Burger, 1991). Anthropogenic activities causing disturbances include deliberate activities of persecution as well as casual intrusions and other activities that are not always directed at forest animals. The causal relationship between human disturbances and adverse effects on animal populations is inherently difficult to demonstrate and therefore has been under-reported in the literature (Nisbet, 2000). However, it is evident that deforestation in many tropical forests has created a distinct forest-farmland interface with heavily degraded edge habitats that have exposed interior forest animal populations to regular disturbances.

Threats from increased predators and associated stress from threats due to human-wildlife conflict can affect the dynamics of wild animal population or change their social structure and behavior (Beissinger, 1997; Clemmons & Buchholz, 1997; Phillips & Alldredge, 2000). Social structure is a key component in the evolution and dynamics of social species such as primates. Social disruption can have a considerable effect on population performance even if it does not directly impact species survival and reproduction. Edge disturbances in particular may force animal species to sacrifice other components of their fitness (i.e. feeding and socializing) by spending time travelling and being vigilant or foregoing opportunities in risky habitats (Kotler & Holt, 1989; Houston et al., 1993). This trade-off between safety, food, and group cohesion ultimately affects population performance (McNamara & Houston, 1987).

An analysis of how a species distributes its time among various behavioral activities and survival strategies is an essential precursor to understanding the interrelations between disturbed habitats and species ecology, behavior, and survival (Struhsaker & Leland, 1979). Certain primate species undergo radical behavior changes such as developing self-protective tactics against threats (Gautier-Hion et al., 1981; Treves, 1999; Enstam, 2002). For example, before raiding crops, vervet monkeys (*Chlorocebus aethiops*) cease to give loud calls, and while some members of the group invade crops, others remain on alert at the forest edge where they might warn crop raiders in case of danger (Fedigan & Fedigan, 1988).

Species living on forest edges are likely affected by a complex array of direct or indirect edge disturbances (Murcia, 1995; Fahrig, 2003; Siex, 2003; Irwin, 2008). A few studies have so far evaluated edge effects on primate distribution (Marsh, 2003; Olupot, 2004; Mbora & Meikle, 2004; Lehman et al., 2006) and only a handful of studies have systematically investigated edge effects on the behavioral ecology of primates (e.g. Gathua, 2000; Irwin, 2008). These studies have found that a trade-off is necessary for animal species to allocate required time and energy to behavioral activities and to carry out survival adjustments. This study examined responses of l’Hoest’s monkeys (*Cercopithecus lhoesti*) to variation in disturbance regimes following an edge-interior forest gradient in a multiple use zone (MUZ) in Bwindi Impenetrable National Park in southwestern Uganda. L'Hoest's monkeys have been shown to be restricted to mature forest and susceptible to disturbances in the Kibale forest, Uganda (Smuts et al., 1987), while in the Bwindi forest, they frequent disturbed edge habitats and regularly raid crops outside the park (Butynski, 1985; McNeilage et al. 2001; Baker, 2004; Andama, 2007). The l'Hoest's monkey in the Bwindi forest is therefore an excellent model for investigating primate species adaptive behavior to edge effects (see Yahner, 1988; Ferreira & Laurance, 1997). A few studies have found that forest edges in Bwindi are associated with a prevalence of threats such as terrestrial and aerial predators and parasites (Andama, 2000; Kalema-Zikuzoka et al. 2002). Furthermore, there is a rising problem of human-wildlife conflicts around the park due to high human population density and the proximity and accessibility of agricultural crops to wildlife inside the park (Baker, 2004; Andama, 2007). I assessed whether and when the activity budgets of l'Hoest's monkeys differed among edge zones and between the edge and the interior of the Bwindi forest. I compared behavioral patterns between edge and interior groups and explored how threats from the surrounding matrix affect the ranging behavior and survival strategies of l'Hoest's monkeys in the Bwindi forest. When there were differences, I speculated on reasons that caused them. Understanding the impact of edge disturbances on survival of l'Hoest's monkeys and on their ranging and social behavior is an important step towards the management of fragmented landscapes and the conservation of species living on forest edges.

METHODS

Study site

Bwindi Impenetrable National Park, hereinafter “Bwindi” is believed to hold the richest faunal community in East Africa, including over 214 species of forest birds (336 species in total), 120 species of mammals (including 7 species of diurnal primates), and 202 species of butterflies (84% of the country's total) (UNEP-WCMC, 2003). Bwindi has been recognized as a very important site for the conservation of Afromontane fauna, in particular those endemic to the Albertine Rift, including mountain gorillas (*Gorilla g. beringei*) and l’Hoest’s monkeys (*Cercopithecus lhoesti*). The park is essentially an island forest in a sea of small farmlands in one of Uganda’s most densely populated rural areas, with an average of 227 people/km^2, nearly three times the current national density (Baker, 2004). Referring to the Ugandan National Bureau of statistics, Twinomugisha (2007) reported a population density as high as *ca.*700 people/km^2 in adjacent Kisoro District.

These high densities of subsistence agricultural communities obviously have a tremendous impact on the forest ecosystem and its animal diversity, especially at the interface between the forest and farmlands. Even in areas where population densities are low, encroachment on state lands is a common practice in Uganda (Kayanja & Byarugaba, 2001). Human disturbances to monkey populations in Bwindi include hunting of crop raiding animals using dogs, children throwing stones at monkeys from forest trails, and people making noise on their way to churches, markets, or other functions, in addition to the indirect effects of woodcutting and other non-timber forest product collection. Inside Bwindi forest most disturbances occur in the multiple use zones (MUZs) which were established mainly near the park boundaries to help ease tension between park management and local populations (Bitariho et al., 2006). MUZs are mostly used by beekeepers, who sometimes carry out illegal activities in the park, including cutting poles, hunting and setting traps for forest duikers (*Cephalophus* spp.) and small mammals, and collecting medicinal plants and other non-timber forest products.

Study species

The l'Hoest's monkey (*Cercopithecus lhoesti*, Figure 1) is one of several relatively unknown species in the *Cercopithecus* genus. According to Kingdon (1997), the combination of shyness, terrestriality, relatively quiet behavior, and difficulties of habituating and following l'Hoest's monkeys in rugged habitats may explain why the species has been less studied. L'Hoest's monkey is a semi-terrestrial species whose geographical distribution is restricted to montane forests in western Burundi, Rwanda, and Uganda, and to montane and mature lowland forests in the eastern Democratic Republic of Congo (Lernould, 1988; Boitani et al., 1996; Kaplin & Moermond, 2000; Gautier et al., 2002; Kaplin, 2002). L'Hoest's monkey is also listed as a near-threatened species on the Red List of the World Conservation Union (IUCN, 2008). Predators of l'Hoest's monkeys in Bwindi include feral dogs, jackals, golden cats, and crowned-hawk eagles (*Stephanoetus coronatus*). Baboons and chimpanzees can also threaten the species and affect their social structure and behavioral patterns.

Figure 1. An adult female l’Hoest’s monkey with her infant in the Bwindi forest.
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Behavioral data collection

An edge group and an interior group of l’Hoest’s monkeys of approximately 36 and 18 individuals respectively were habituated for nine months (from October 2005 to June 2006), after which behavioral data were collected from July 2006 to February 2007 and from May to September 2007. To avoid a possible confounding variable that can result from different observers, all behavioral data were collected only by me. I was not able to recognize individual monkeys; therefore, I classified them according to their age classes, although the lone mature adult male was recognizable by a blue scrotum and sub-adult males were distinguished from other adult individuals by their black scrotums. Behavioral activity data were recorded using the instantaneous scan sampling method (Altmann, 1974; Martin & Bateson, 1986). I scanned the group for two minutes and recorded the first activity sustained for at least five seconds by each visible individual

(Kaplin & Moermond, 2000). An intermission of three minutes between scans allowed me to keep up with the monkeys and take ad libitum observations. In this manner, 12 scans were performed each hour.

Activities recorded included feeding, a category in which I combined feeding and foraging or reaching out for, picking, or manipulating food items, or placing food in the mouth. I also recoded food part, i.e. fruit, flowers, leaves, insects, animal matter and other, and when possible identified to species each food item each monkey observed was eating. Additional activities recorded were resting (when the animal was stationary and not involved in any apparent activity); moving, including traveling, running, jumping, climbing and balancing on branches; socializing, including grooming or the examination and cleaning of one monkey (the groomer) by another (the groomee), and playing; vocalizing including contact and alarm calls; vigilance, which involves sitting or standing (stationary) with the head in constant multidirectional motion while apparently searching nearby vegetation for food or scanning the environment, usually in one direction, beyond arm’s reach in response to perceived or real threat; and ‘other”, a category of activities that included rare events (i.e., urinating, mating, nursing, displaying, giving birth) (Butynski, 1990; Treves, 1999; Kaplin & Moermond, 2000; Enstam, 2002; Di Fiore, 2003). I also recorded four main disturbance agents: presence of people (encroaching in the forest or defending their farms over crop raiders), presence or calls of aerial (crowned eagle) and terrestrial (feral dogs, jackals, golden cats) predators, and encounters with conspecific groups and other threatening species, including encounters with baboons, chimpanzees, gorillas, and snakes.

Ranging data

The edge group ranged between *ca* 500 m outside the park to about 400 m from the park boundary towards the forest interior, while the interior group ranged between 600 m and 2200 m in the interior forest. Ranging data were collected on each of the two habituated groups for up to 6 days a month. Since groups were very well habituated, it was possible to record Global Positioning System (GPS) points of each ‘estimated center of mass’ of a followed group (Cords, 1984; Kaplin & Moermond, 2000) every 30 minutes. For each full day of data collection (730-1830 hours), a daily travel path was created using ArcView 3.2 (see Siex, 2003). Fixed Kernel analysis, the extension of the home range analysis, was used to calculate the area of the home range used by both groups of l’Hoest’s monkeys. Daily path lengths were determined based on the distance in meters from one sleeping site to the next through several consecutive but non-linear GPS points. L’Hoest’s monkeys could use the same sleeping site for several consecutive nights. A sleeping site was characterized by a group of trees, lianas, and shrubs forming enough leaf cover as a shelter against rain and nocturnal predators (Vié et al., 2001). Sleeping sites were usually located near fruiting trees and near crops on hill sides or hill tops in dense leaf cover and were reused several times over the course of the study.

Data analysis

Activity records were used to assess and compare the amount of time (percentage) spent on each activity among edge zones and between the edge and interior groups. The ranging of the edge group and edge data were stratified into four zones (outside the forest, on the edge 0 to 50 m, near the edge 50 to 250 m and away from the edge or over 250 m from the edge towards the interior forest (Figure 2). The location of each activity was attributed to the closest GPS point taken within the last 30 minutes of the activity.

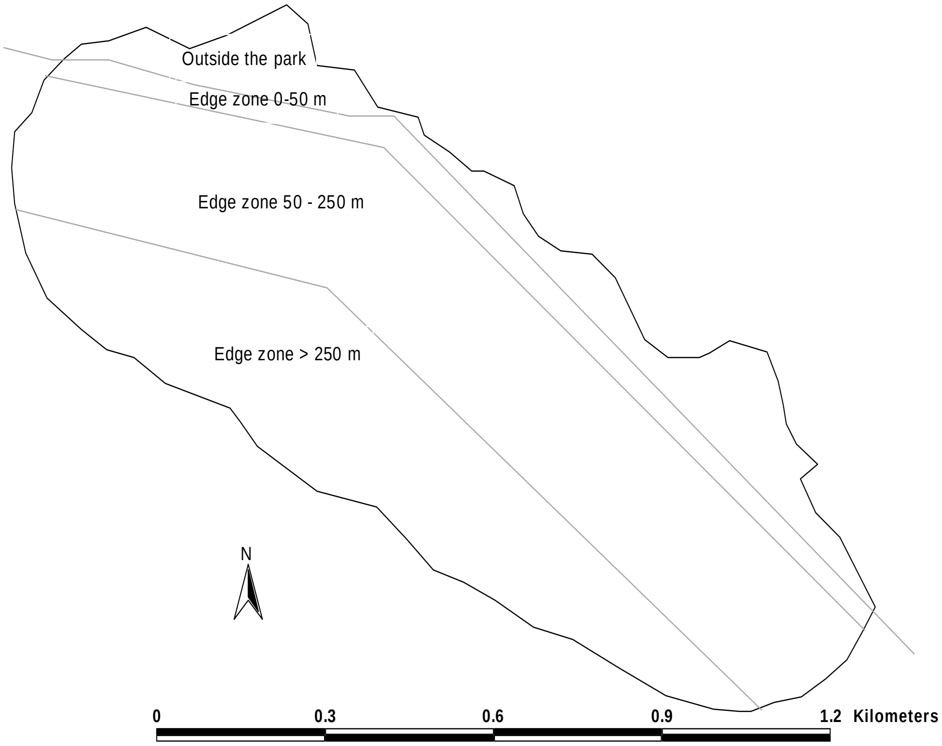

Figure 2. Illustration of the stratification of the home range of the edge group of l'Hoest's monkeys into four difference zones in the Bwindi forest.

Geographical data were analyzed in ArcView 3.2. The paired-samples t-test and the Friedman chi-square-test were used to detect differences between monthly records of behavioral variables and activity budgets between the edge and interior groups of l'Hoest's monkeys and among different edge zones including the matrix, 0 to 50 m, 50 to 250 m and > 250 m zones (Figure 2).

I used stepwise linear regression (SLR) to determine which variables (encounters with people, aerial and terrestrial predators, and time spent outside the park) had the greatest influence on each group's behaviors or daily path lengths. An independent variable that contributed to the increase or decrease in daily path length was determined by how much R^2 increased after that variable was retained in the model. Each relationship was illustrated as a simple regression on a scatter plot. Pearson correlation was also utilized to test the relationship between daily path lengths and the presence of baboons and apes. The t-test and SLR were computed for relationships whose residuals were normally distributed. All statistical tests were run on SPSS 16.0 (SPSS Inc., Chicago, USA).

RESULTS

Activity budgets and ranging ecology of l'Hoest's monkeys in Bwindi

L'Hoest's monkeys were followed for a total of 69 days (edge group) and 71 days (interior group) tallying to 1242 human-hours with 7474 and 7430 scans for the edge and interior groups respectively (Table 1).

Table 1. Number of scans per month sampled in the interior and edge groups of l'Hoest's monkeys in the Bwindi forest

	Edge		**Interior**	
Month	**No. scans**	**n (days)**	**No. scans**	**n (days)**
Jul-06	444	4	269	4
Aug-06	639	6	582	6
Sept-06	244	2	360	4
Oct-06	637	6	645	6
Nov-06	653	6	648	6
Dec-06	673	6	704	6
Jan-07	752	6	696	6
Feb-07	633	6	657	6
May-07	736	6	767	6
June-07	457	5	463	5
Jul-07	483	5	593	5
Aug-07	547	5	436	5
Sept-07	576	6	610	6
Overall	**7474**	**69**	**7430**	**71**

There were no significant differences in behavioral activities (Table 2) between the edge and interior groups when comparing the percentage of records of feeding, resting, travelling, vigilance, and vocalizing. Only socializing and ‘other’ activities occurred significantly more frequently in the interior group than in the edge group (Social activities: t = -2.691, p = 0.02, df = 12; ‘other’ activities: t = -3.758, p = 0.003, df = 12). However, both activities represented a small proportion (4 % and 1% respectively) of the total activity budget of l’Hoest’s monkeys in the Bwindi forest (Table 2).

Table 2. Proportion of time spent in different activities across all months sampled in the edge group and interior groups of l’Hoest’s monkeys in the Bwindi forest.

Activity	**Edge group x ± s.d.**	**Interior group x** ± s.d.	**t statistic**	**p value**
Feeding	34 ± 2.54	33 ± 3.9	0.955	0.36
Resting	24 ± 6.74	23 ± 4.41	0.695	0.5
Socializing	4 ± 1.3	5 ± 1.29	-2.691	0.02*
Moving	30 ± 5.1	31 ± 4.32	-1.427	0.18
Vigilance	3 ± 1.34	2 ± 0.92	1.567	0.14
Vocalizing	4 ± 1	4 ± 1.12	0.718	0.49
Other	1 ± 0.05	2 ± 0.05	-3.758	0.003*

The table includes the mean of activity records ± standard deviation (x ± s.d.) and the paired samples t-tests for each activity with df = 12. * indicates significant difference, $p < 0.05$.

There was no significant difference in the percentage of occurrence of the four main disturbance agents (people, aerial predators, terrestrial predators, and contact with conspecifics) between the edge and interior groups (Friedman $\chi^2 = 0.077$; 0.333; 0.333 and 0.692 with p = 0.782; 0.564; 0.564 and 0.405 respectively and n = 13 for the four tests) (Table 3). However, some behavioral activities were differently affected by some disturbance agents. For example, the step-wise linear regression analysis did not find any significant effect on behaviors measured in the edge group due to the presence of aerial predators or people. However, the presence of aerial predators resulted simultaneously in the increase in time spent in behaviors in the ‘other’ category (i.e. urinating, defecating and other rare activities) and a decrease in time spent feeding ($R^2 = 0.637$, $F_{2, 10} = 11.517$, $p = 0.003$) in the interior group. The presence of people corresponded with a decrease in time spent resting for the interior group ($R^2 = 0.420$, $F_{1, 11} = 7.972$, $p = 0.017$) (Table 3, Figures 3, 4 & 5).

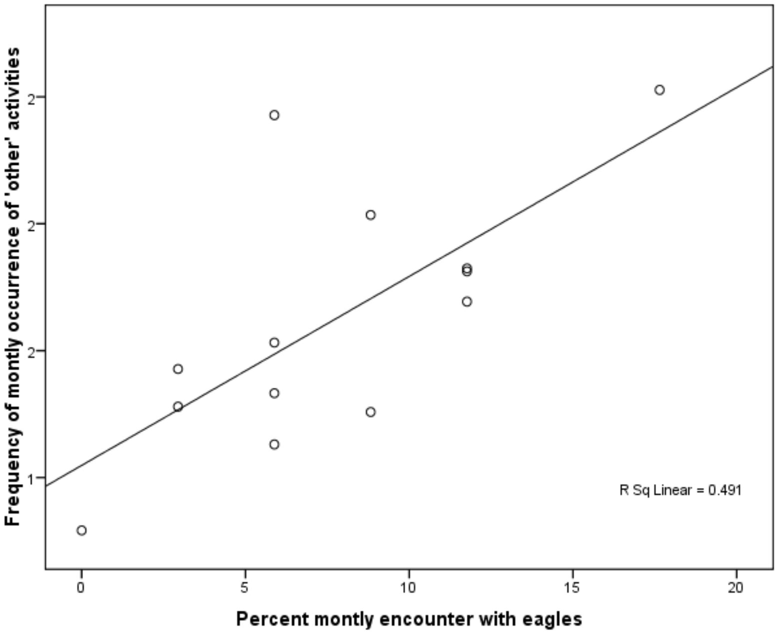

Figure 3. The relationship between aerial predators and time spent in ‘other’ activities by l’Hoest’s monkeys of the interior group in the Bwindi forest.

Table 3. Monthly home range size, daily path lengths, percentage of observations outside the park, and contact with disturbance agents in the edge (E) and interior (I) groups of l'Hoest's monkeys.

Month	Home range (ha) (Kernel 95%)		Mean daily path length ± s.d. (m)		Time spent outside the park		Contacts with conspecific groups		Contact with people		Contact with aerial predators		Contact with terrestrial predators	
	E	I	E	I	E	I	E	I	E	I	E	I	E	I
Jul-06	36	37	2368 ± 277	1591 ± 172	0	0	0	4.4	8.6	8.7			8.6	4
Aug-06	41	37	2591 ± 549	1691 ± 559	4.8	0	7.1	4.4	14.3	13	10	2.9	14.23	4
Sep-06	40	25	2479 ± 445	2173 ± 343	0	0	7.1	8.7	0	17.4	10	11.8	0	0
Oct-06	28	34	1886 ± 296	1997 ±336	9.5	0	7.1	8.7	5.7	8.7	5	5.9	5.7	12
Nov-06	47	33	2264 ± 156	1826 ± 364	9.52	0	7.1	17.4	5.7	8.7	15	8.8	5.7	8
Dec-06	55	40	2205 ±365	1662 ± 229	9.52	0	7.1	4.4	11.4	8.7	15	5.9	11.4	16
Jan-07	79	28	2115 ± 346	1104 ± 185	11.9	0	7.1	4.4	8.6	0	5	11.8	8.6	16
Feb-07	49	21	1880 ± 469	1416 ± 425	11.9	0	0	4.4	2.9	0	20	17.7	2.9	12
May-07	54	37	2415 ± 646	1953 ± 280	9.5	0	28.6	8.7	14.3	13	5	11.8	14.3	4
Jun-07	41	35	2331 ± 358	1962 ± 432	9.5	0	0	4.35	8.6	8.7	5	5.9	8.6	4
Jul-07	46	37	2368 ± 277	1324 ± 112	7.1	0	0	8.7	2.9	8.7	10	2.9	2.9	4
Aug-07	49	33	1823 ± 541	1480 ± 259	9.5	0	7.1	8.7	8.6	0	0	5.9	8.6	4
Sep-07	57	36	1932 ± 471	1602 ± 161	7.1	0	21.4	13	8.6	4.3	0	8.8	8.6	12
For 13 months	71	52			42	0	14	23	35	23	20	34	20	25
Mean ± s.d.	49 ± 12	33 ± 6	2218 ± 269	1676 ± 303	9 ± 2	0	11 ± 8	8 ± 4	8±4	10±4	10 ± 5	8 ± 4	8 ± 4	8±5

s.d. = standard deviation

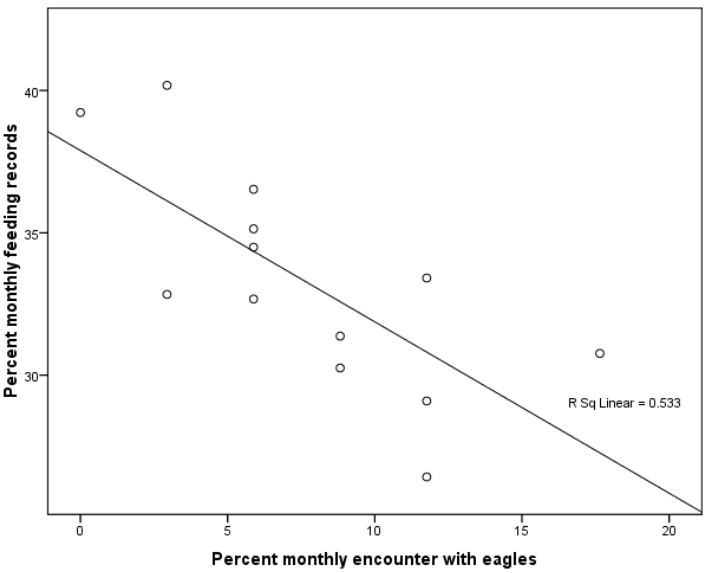

Figure 4. The relationship between aerial predators and time spent feeding for l’Hoest’s monkeys of the interior group in the Bwindi forest.

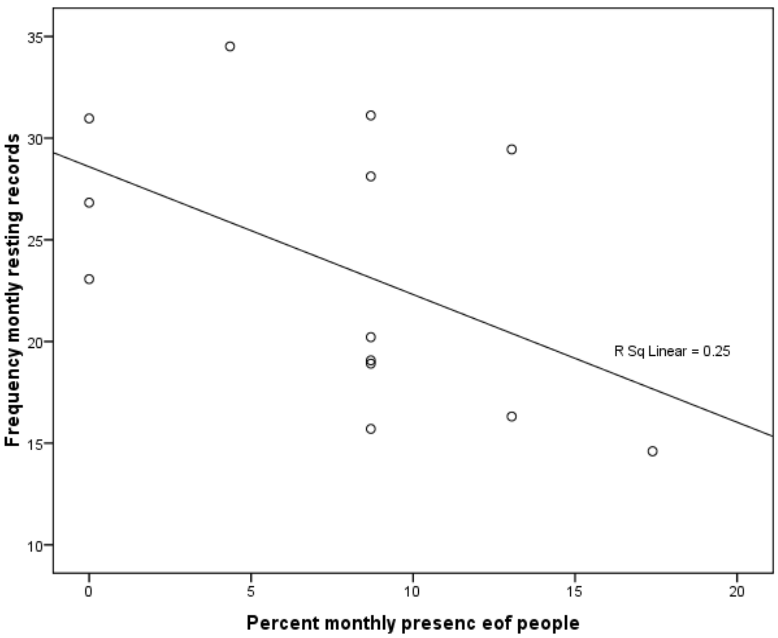

Figure 5. The relationship between time spent resting and the presence of people in the interior group of l’Hoest’s monkeys in the Bwindi forest.

During the 13 months of the study, the edge group had significantly longer mean daily path lengths (DPL) (2218 ± 269 m) than the interior group (1676 ± 303 m) (t =

5.768, $p = 0.0001$, $df = 12$). The longest DPL (3211 m) was recorded on 12 May 2007, a day after a new adult male had taken over the edge group. The Fixed Kernel estimated a significantly larger home range for the edge group (48 ± 12 ha) than the interior group (33 ± 6 ha) ($t = 3.765$, $p = 0.003$, $df = 12$). October 2006 was the only month when the interior group had a larger home range and longer daily path than the edge group (Table 3).

The DPL decreased when the frequency of going outside the park increased ($R^2 = 0.319$, $F_{1, 12} = 5.164$, $p = 0.044$) (Figure 6). Going outside the park was an exclusive activity of the edge group. Among other disturbances, the edge group rarely came into contact with gorillas and chimpanzees (3 times) but was frequently threatened by baboons (11 times). The interior group came into contact with apes 20 times during my study. However, there was no relationship between DPL and the encounter rates with baboons and/or chimpanzees and mountain gorillas (apes) in the edge and interior groups (Pearson correlation $r = -0.006$, $p = 0.984$ and $r = -0.445$ and $p = 0.128$ respectively, $n = 13$ in both correlations). The presence of people in the forest resulted in an increase in DPL and a decrease in resting time ($R^2 = 0.578$, $F_{1, 12} = 15.079$, $p = 0.003$) (Table 3, Figures 5 & 7).

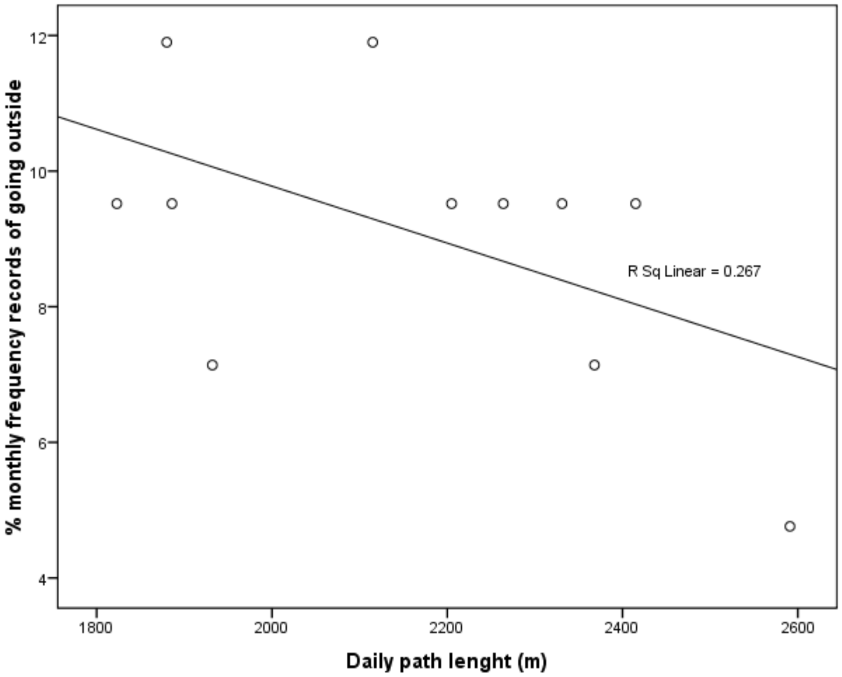

Figure 6. The relationship between mean daily path length and proportion of observations outside the park each month for the edge group of l'Hoest's monkeys in the Bwindi forest.

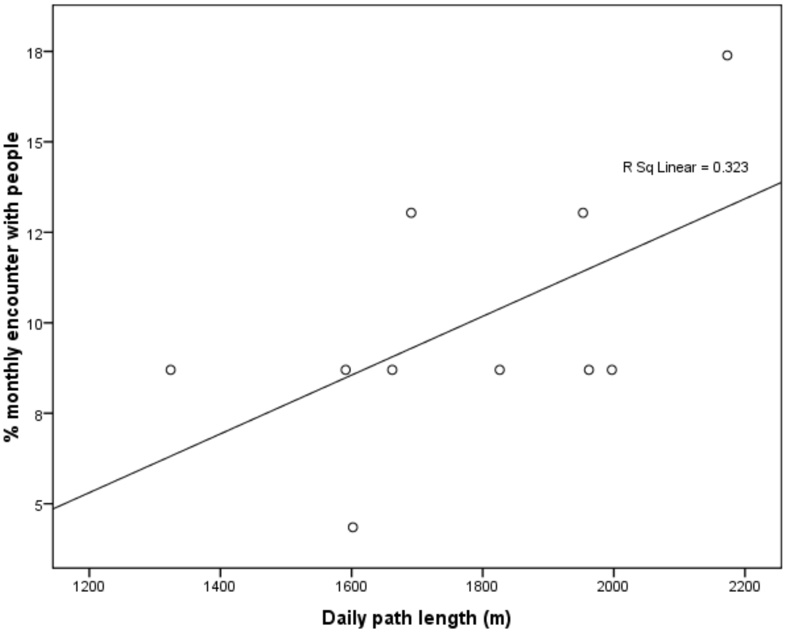

Figure 7. The relationship between mean daily path length and encounters with people inside the Bwindi forest in the interior group of l'Hoest's monkeys.

Matrix effect on the ranging and feeding ecology of the edge group of l'Hoest's monkeys

Feeding was the main activity (36%) of l'Hoest's monkeys when they were outside the park, where they spent only about 8% of their time compared with other zones stratified in the edge group home range (Figures 8 and 9). L'Hoest's monkeys were attracted by local crops but also fed substantially on indigenous terrestrial vegetation growing in fallows.

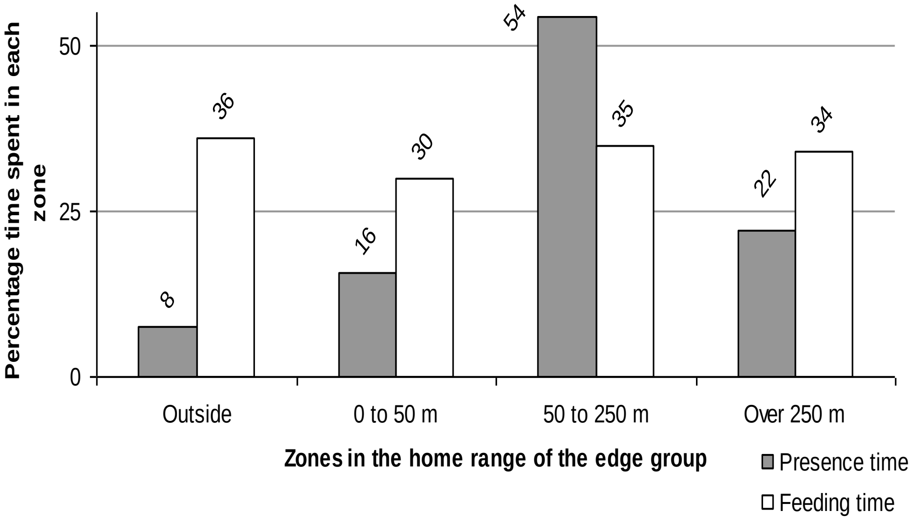

Figure 8. The proportion of time spent in each zone of the home range of the edge group of l'Hoest's monkeys and proportion of time spent feeding within each zone in the Bwindi forest. The numbers over each bar are percentages of observation records.

Although there was no sleeping site outside the park boundary, l'Hoest's monkeys of the edge group slept close to farms of crops (e.g. beans, corns, potatoes, and sorghum). Out of 14 sleeping sites I observed during the study, five sleeping sites (sites 1, 2, 3, 12, 13) were used for over 52% of the 69 nights recorded for the edge group (Figure 9), mostly as bases for foraging outside the park and raiding crops. Monkeys usually invaded crops very early in the morning or very late in the evening, before the farm guards arrived or after they had left.

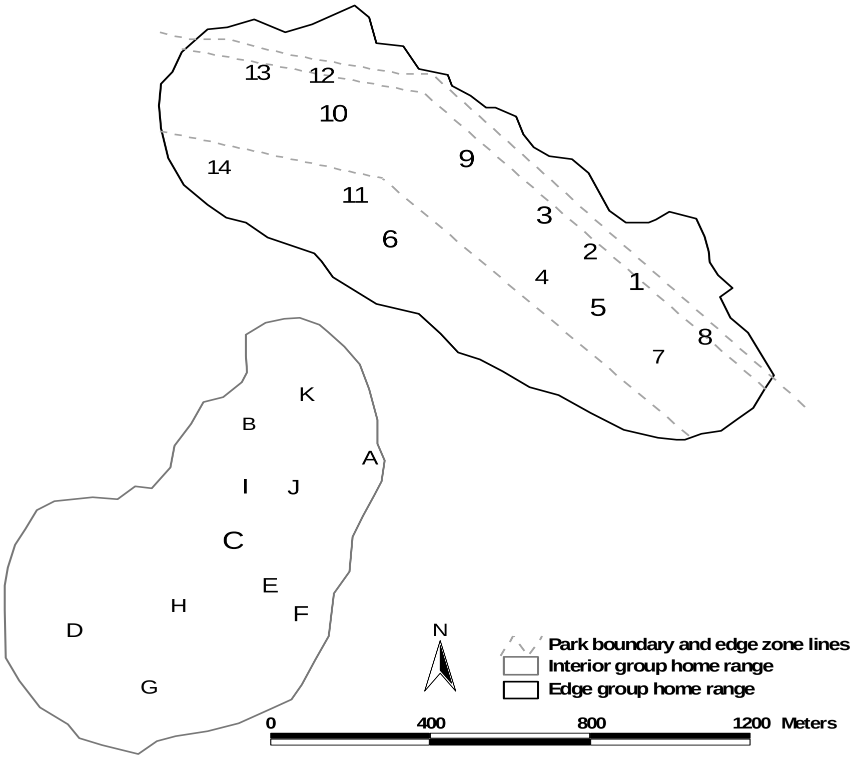

Figure 9. Sleeping sites of the edge and interior groups of l'Hoest's monkeys in the Bwindi forest. The dotted lines divide the edge group home range into outside, 0-50 m, 50-250 m and > 250 m zones. Each new sleeping site was consecutively recoded either numerically (edge group) or alphabetically (interior group) from 1 to 14 or A to K respectively.

Edge-related disturbance effects on l'Hoest's monkeys' group composition

In total 11 infants were born in the edge group and 13 in the interior group, including five infants present in the edge and four in the interior group at the beginning of data collection. Births occurred throughout the year but were mostly clumped around the end of wet seasons in December and June. I recorded two individual (11%) disappearances in the interior group: a female that had been dominant throughout the study and an infant that was born during the long dry season. In the edge group, eight individuals (22%) were presumably killed: three adults by hunters and one adult male by farm guards (according to local informants), one infant by a crowned eagle, and 3 infants probably victims of infanticide by new adult males.

Additionally, within the course of this study, four sub-adult males left the interior group and over seven left the edge group. Overall, the edge group membership declined from *ca* 36 individuals to *ca* 26 during my study, while the interior group declined from 18 to 14 individuals by the end of the study period.

DISCUSSION

Effects of disturbances on the behavioral and ranging ecology of the edge and interior forest groups of l'Hoest's monkeys in the Bwindi forest

One of the most striking findings of this study was the similarity in amount of time devoted to behavioral activities including vigilance in the edge and interior groups of l'Hoest's monkeys. I expected there to be differences in behaviors such as vigilance, if edge effects were influencing the monkeys that range along the forest edge. The lack of difference may be explained by the fact that both groups could be experiencing similar levels of edge effects and disturbances. Edge effects may penetrate deep into the Bwindi forest. A study by Olupot (2004) found edge effects to influence the distribution and behavior of mammals up to over 2,000 m inside Bwindi forest. Past logging in the forest (until 1991) has altered forest structure and composition, and much of the forest where both groups ranged near the park bondary is likely a secondary forest in its early successional stages (pers. obs.).

The interior group did allocate more time to social and ‘other’ activities than the edge group. Although both activities accounted for less than 6% of the total activity budget in either group, not investing in social activities could be related to edge effects (Phillips & Alldredge, 2000). Trading social behaviors for other activities could have a considerable effect on the group cohesion of social species such as primates (McNamara & Houston, 1987).

The distribution and occurrence of disturbances did not differ significantly between the edge and the interior home ranges of l’Hoest’s monkeys in the Bwindi forest. Anthropogenic activities have been reported to be widespread throughout the Bwindi forest (Butynski, 1984; Kayanja & Byarugaba, 2001) and were commonly observed in the edge and interior groups of l’Hoest’s monkeys in this study. Disturbances from predators did not differ, which is not so surprising since large animals, especially carnivores (jackals, golden cats, and raptors), have large home ranges that could overlap with (Woodroffe & Ginseberg, 1998) and impose the same level of threat towards both groups of l’Hoest’s monkeys. The only variation in the distribution of recorded disturbances was that of baboons and feral dogs, which were exclusively found on the forest edge, while great apes (chimpanzees and mountain gorillas) were encountered more frequently in the forest interior. Such distribution of baboons and apes concurs with the findings of Olupot (2004).

Despite the similarities in the distribution of disturbances between the edge and interior home ranges of l’Hoest’s monkeys in the Bwindi forest, the groups responded differently to certain disturbances. Generally, the daily paths and home ranges of the edge group were longer and larger respectively than those of the interior group. However, being outside the park resulted in a reduction of daily path lengths for the edge group. In October 2006, for example, the mean daily path length and monthly home range size of the edge group were shorter and smaller respectively than those of the interior group because the edge group spent much time stationary near the forest boundary waiting for a chance to raid bean fields outside the park. The daily path lengths of the interior group increased with an increase in human presence in the park. Burger (1991) and Nisbet (2000) recognized that human activities have adverse effects on animal behavior and fitness. L'Hoest's monkeys usually responded to human disturbances by (1) running away and covering long daily distances, or (2) staying stationary, apparently to avoid contact with humans, especially in the vicinity of the forest edge before or after crop raiding.

Matrix effects on the ranging ecology of l'Hoest's monkeys in the Bwindi forest

Daily path lengths decreased significantly when the edge group went outside the park. Despite the risky nature of feeding on local crops, l'Hoest's monkeys in the edge group spent time feeding on this resource using various behavioral strategies. Before going out of the forest, these l'Hoest's monkeys spent a lot of time waiting and making sure it was safe to venture into the farmlands and abandoned fields. Before raiding crops, the l'Hoest's monkeys adopted the strategy of the edge thriving vervet monkey species, described by Fedigan and Fedigan (1988): while adults were raiding crops, juveniles were more cautious and remained vigilant in trees on the forest, where they warned crop raiders of any danger, especially the presence of farm guards.

Crops are usually abundant and are believed to be high quality food. Therefore, the distribution, quality, and quantity of food can significantly influence the ranging behavior and movement of primate groups (Enstam, 2002). As the landscape became more fragmented by anthropogenic activities, the proximity and accessibility of humans to natural resources and wildlife to local subsistence crops also increased, causing intense human-wildlife conflicts. These conflicts are serious direct threats to the dynamics of the wildlife populations (survival and reproduction), whereas behavioral change can be considered of lesser importance (Beissinger, 1997; Clemmons & Buchholz, 1997). This study contributed to the assessment of the impact of matrix habitat on the behavioral ecology of l'Hoest's monkeys. Thus, once behavioral patterns of animal species are disrupted, it is likely that their population dynamics will also be altered (McLellan & Shackleton, 1989, Phillips & Alldredge, 2000).

Edge versus interior group composition in l'Hoest's monkeys of the Bwindi forest

The results of this study illustrated negative forest edge effects. Edge disturbances can have negative impact on birth rates, survivorship, and other demographic parameters of edge groups of primates (Singh et al., 2001). Wong and Sicotte (2007) reported that primate groups living on the edges of tropical forests experience high levels of human harassment. Edge effects resulting from habitat loss are one of the leading causes of recent population declines and species extinctions (Irwin, 2008). Johns and Skorupa (1987) evaluated responses of primate species to habitat disturbances and found that of the 38 primate species examined throughout the tropics, 71% showed an appreciable decline in numbers, 22% increased, and only about 7% showed no change.

Besides measurable variables such as number of births and deaths, there may be many subtle factors that could threaten populations (Irwin, 2008). These factors are all contributors to edge effects and include lower-quality diet, reduced body mass, energetically costly activities, and diseases. Edge groups may exploit higher density resources found in edge-affected forest, but these resources may be lower in quality, causing stress to species and setting an ecological trap (Lehman et al., 2006; Irwin, 2008). Therefore, forest edges may become population sinks due to negative edge effects and other threats towards l'Hoest's monkey. It is therefore timely for concerted conservation measures to protect primates living on forest edges, where their survival is threatened by many disturbances.

CONCLUSION

Determining ecological and demographic constraints based on activity budgets is key to understanding the socio-ecology and conservation of primate species. In the Bwindi forest, l'Hoest's monkeys living along the edge did not appear to be more affected behaviorally by edge effects than an interior group. Both groups spent equivalent amounts of time on the major behavioral activities such as feeding, travelling, and resting. However, concerning ranging, I observed an increase in the edge group's daily path lengths and home range sizes compared with these of the interior group. Nevertheless, while crop raiding or foraging outside the park, l'Hoest's monkeys of the edge group remained stationary for long periods of time, apparently to ensure it was safe to go out of the park into the surrounding matrix. Crop raiding days were therefore characterized by shorter paths travelled by the edge group. Crop raiding was a very risky activity during which l'Hoest's monkeys experienced more direct casualties. Human retaliation following crop raiding accounted for half of the monkeys killed in the edge group.

As edge effects will always characterize the interface between forests and farmlands and edge-related threats will not be eliminated in the near future, long-term stressful edge conditions could result in population decline and irreversible extinction of species living on forest edges (Cowlishaw, 1999). In order to conserve l'Hoest's monkeys and protect farmers' crops, a buffer zone of abandoned farmlands between the forest and the cropland would be an effective barrier (Andama, 2007). If such a buffer cannot be left alone to regenerate, it should at least be used only for grazing livestock. A detailed study should be undertaken around Bwindi to assess the effective size of such buffer zones in relation to aspects of the landscape and the type of crops planted in the matrix. Additionally, planting corn, sorghum, beans, peas and potatoes right on the forest edge should be discouraged as long as an alternative can be provided for the farmers. Once anthropogenic disturbances to wild populations are effectively controlled, these populations could have the ability to recover and become resilient (Shively et al., 2005).

LITERATURE CITED

Altmann J. 1974. Observational study of behavior: sampling methods. *Behavior* 49:227-267.

Andama E. 2000. *The status and distribution of carnivores in Bwindi Impenetrable National Park, south-western Uganda*. Thesis. Makerere University. Kampala. Uganda.

Andama E. 2007. *Invasive potential of Mauritius thorn (Cesalpinia decapetala) (Roth) Alston and its use to deter crop raiding by wild animals around Bwindi Impenetrable National Park, Uganda*. Dissertation. Makerere University.

Baker J. 2004. *Evaluating conservation policy: Integrated conservation and development in Bwindi Impenetrable National Park, Uganda*. Dissertation. University of Kent. UK.

Beissinger, S.R. 1997. *Integrating behavior and conservation biology: potentials and limitations*. In Clemmons J.R. & R. Buchholz (Eds.). *Behavioral approaches to conservation in the wild*. Cambridge University Press. Cambridge. UK. Pp. 3-22.

Bitariho, R., A. McNeilage, D. Babaasa & R. Barigyira. 2006. Plant harvest impacts and sustainability in Bwindi Impenetrable National Park, S.W. Uganda. *Journal of African Ecology*. 44: 12-21.

Boitani L., F. Corsi, A. De Biase, I.D. Carranza, M. Ravagli, G. Reggiani, I. Sinibaldi & P. Trapanese. 1998. *A databank for the conservation and management of the African mammals. A guide to the methods and data.* Institute of Applied Ecology. Rome.

Burger J. 1991. Foraging behavior and the effects of human disturbance on the piping plover (*Charadrius melodus*). *Journal of Coastal Research* 7: 39-52.

Butynski T.M. 1984. *Ecological survey of the Impenetrable (Bwindi) forest, Uganda, and recommendations for its conservation and management*. New York Zoological Society. New York.

Butynski T.M. 1985. Primates and their conservation in the Impenetrable (Bwindi) Forest, Uganda. *Primate Conservation* 6: 63-72.

Butynski T.M. 1990. Comparative ecology of Blue monkeys (*Cercopithecus mitis*) in high and low density subpopulations. *Ecological Monographs* 60: 1-26.

Clemmons, J. R. & R. Buchholz. 1997. *Linking conservation and behavior.* In Clemmons J. R. & R. Buchholz (Eds.). *Behavioral approaches to conservation in the wild*. Cambridge University Press. Cambridge. UK.

Cords M. 1984. Mating patterns and social structure in redtail monkeys (*Cercopithecus ascanius*). *Zeitschrift fur Tierpsychologie* 64: 313-329.

Cowlishaw G. 1999. Predicting the patterns of decline of African primate diversity: an extinction debt from historical deforestation. *Conservation Biology* 13: 1183-1193.

Di Fiore A. 2003. Ranging behavior and foraging ecology of lowland woolly monkeys (*Lagothrix lagotricha poeppigii*) in Yasuní National Park, Ecuador. *American Journal of Primatology* 59: 47-66.

Enstam K.L. 2002. *Behavioral ecology of perceived risk of predation in sympatric Patas (Erythrpcebus patas)* and *Vervet (Cercopithecus aethiops) monkeys in Laikipia, Kenya*. Dissertation. University of California. Davis.

Fahrig L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Evolution and Systematics* 34: 487-515.

Fedigan L. & L.M. Fedigan. 1988. *Cercopithecus aethiops: a review of field studies*. In Gautier-Hion A., F. Bourlière & J.-P. Gautier. *A primate radiation: evolutionary biology of the African guenons*. Cambridge University Press Cambridge. Pp. 389-411.

Ferreira L.V. & W.F. Laurance. 1997. Effects of forest fragmentation on mortality and damage of selected trees in central Amazonia. *Conservation Biology* 11: 797-801.

Gathua J.M. 2000. *Intraspecific variation in foraging patterns of redtail monkeys (Cercopithecus ascanius) in the Kakamega Forest, Kenya*. Dissertation. Columbia University.

Gautier-Hion A., J.P. Gautier & R. Quris. 1981. Forest structure and fruit availability as complementary factors influencing habitat use by a troop of monkeys (*Cercopithecus cephus*). *Revue Ecologique (Terre et Vie)* 35: 511-536.

Gautier J.P., R.V. Drubbel & P. Deleporte. 2002. *Phylogeny of the Cercopithecus lhoesti group revisited: Combining multiple character sets*. In Glenn M.E. & M. Cords (Eds.). *The guenons: diversity and adaptation in African monkeys*. Kluwer Academic/Plenum Publishers. New York. Pp. 37-48.

Houston A. I., J. M. McNamara & J. M. C. Hutchinson. 1993. General results concerning the trade-off between gaining energy and avoiding predation. *Philosophical Transactions of the Royal Society of London, Series B* 341:375-397.

Irwin M.T. 2008. Diademed sifaka (*Propithecus diadema*) ranging and habitat use in continuous and fragmented forest: higher density but lower viability in fragments? *Biotropica* 40: 231-240.

IUCN 2008. *2008 IUCN Red List of Threatened Species*. www.iucnredlist.org. Downloaded on 20 February 2009.

Johns A.D. & J.P. Skorupa. 1987. Responses of rain-forest primates to habitat disturbance: A review. *International Journal of Primatology* 8: 157-191.

Kalema-Zikuzoka, G.R., D. Kock & E. Macfie. 2002. Scabies in free-ranging mountain gorillas (*Gorilla beringei beringei*) in Bwindi Impenetrable National Park, Uganda. *The Veterinary Record* 150: 12-15.

Kaplin B.A. & T.C. Moermond. 2000. Foraging of the Mountain Monkey *Cercopithecus lhoesti*): Implications for its evolutionary history and use of disturbed forest. *American Journal of Primatology* 50: 227-246.

Kaplin B.A. 2002. *Terrestriality and the maintenance of the disjunct geographical distribution in the lhoesti group*. In Glenn M.E. & M. Cords (Eds.). *The guenons: Diversity and adaptation in African Monkeys*. Kluwer Academic/Plenum Publishers. New York. Pp. 49-60.

Kayanja F. I. B. & D. Byarugaba. 2001. Disappearing forests of Uganda: The way forward. *Current Science* 81: 936-947.

Kingdon J. 1997. *The Kingdon field guide to African mammals.* Academic Press. San Diego.

Kotler B.P. & R.D. Holt. 1989. Predation and competition: the interaction of two types of species interactions. *Oikos* 54:2256–260

Lehman S.M., A. Rajaonson & S. Day. 2006. Edge effects and their influence on lemur density and distribution in Southeast Madagascar. *American Journal of Physical Anthropology* 129: 232-241.

Lernould J.-M. 1988. *Classification and distribution of guenons*. In Gautier-Hion A., F. Bourlière & J.-P. Gautier. *A primate radiation: evolutionary biology of the African guenons*. Cambridge University Press. Cambridge. UK. Pp. 54-78.

Marsh L.K. 2003. *Primates in fragments: Ecology and conservation*. Kluwer Academic/Plenum Publishers. New York.

Martin P. & P. Bateson. 1986. *Measuring behaviour: an introductory guide*. Cambridge University Press. Cambridge.

Mbora D.N.M. & D.B. Meikle. 2004. Forest fragmentation and the distribution, abundance and conservation of the Tana River red colobus (*Procolobus rufimitratus*). *Biological Conservation* 118: 67-77.

McLellan B.N. & D.M. Shackleton. 1989. Grizzly bears and resource extraction industries: habitat displacement in response to seismic exploration, timber harvesting and road maintenance. *Journal of Applied Ecology* 26: 371-380.

McNamara J.M. & A.I. Houston. 1987. The common currency for behavioral decisions. *American Naturalist* 127: 358-378.

McNeilage A., A.J. Plumptre, A. Brock-Doyle & A. Vedder. 2001. Bwindi Impenetrable national Park, Uganda: Gorilla census 1997. *Oryx* 35: 39-47.

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution* 10: 58-62.

Nisbet I.C.T. 2000. Disturbance, habituation, and management of waterbird colonies. *Waterbirds: The International Journal of Waterbird Biology* 23: 312-332.

Olupot, W. 2004. *Boundary edge effects in Bwindi Impenetrable National Park*. Institute of Tropical Forest Conservation. Uganda

Phillips, G. E., & A. W. Alldredge. 2000. Reproductive success of elk following disturbance by human during calving season. *Journal of Wildlife Management* 64:521-530.

Shively K.J., A.W. Allredge & G.E. Phillips. 2005. Elk reproductive response to removal of calving season disturbance by humans. *Journal of Wildlife Management* 69: 1073-1080.

Siex K. 2003. *Effects of population compression on the demography, ecology, and behavior of Zanzibar red colobus monkeys* (*Procolobus kirkii*). Dissertation. Duke University.

Singh M., H.N. Kumara, M.A. Kumar & A.K. Sharma. 2001. Behavioural responses of Lion-tailed macaques (*Macaca silenus*) to a changing habitat in a tropical rain forest fragment in the western Ghats, India. *Folia Primatologica* 72: 278-291.

Struhsaker T.T & L. Leland. 1979. Socioecology of five sympatric monkey species in Kibale forest, Uganda. *Advanced Studies in Behavior* 9: 159-228.

Smuts B., D.L. Cheney, R.M. Seyfarth, R.W. Wrangham & T.T. Struhsaker (Eds.). 1987. *Primate Societies*. University of Chicago Press. Chicago.

Treves A. 1999. Within-group vigilance in red colobus and redtail monkeys. *American Journal of Primatology* 48: 113-126.

Twinomugisha D. 2007. *Conservation status and determinants of Golden monkey (Cercopithecus mitis kandti) abundance in Mgahinda Gorilla National Park*. Dissertation. Makerere University. Uganda.

UNEP-WCMC. 2003. *Protected areas and world heritage: Bwindi Impenetrable National Park*. http://www.unep-wcmc.org/sites/wh/bwindi.html. Downloaded on 1 September 2008.

Vié J.-C., C. Richard-Hansen & C. Fournier-Chambrillon. 2001. Abundance, use of space, and activity patterns of white-faced sakis (*Pithecia pithecia*) in French Guiana. *American Journal of Primatology* 55: 203-221.

Wong S.N.P. & P. Sicotte. 2007. Activity budget and ranging patterns of Colobus vellerosus in forest fragments in central Ghana. *Folia Primatologica* 78: 245-254.

Woodroffe R. & J.R. Ginsberg. 1998. Edge effects and extinction of populations inside protected areas. *Science* 280: 2126-2128

Yahner R.H. 1988. Changes in wildlife communities near edges. *Conservation Biology* 2: 333-339.

CONCLUSION

L’Hoest’s monkeys and forest edge effects

L’Hoest’s monkey species is the first primate species I saw in the wild on the edges of Nyungwe National Park over 19 years ago. My wish at that time was to see all the forest animals and the easiest place to see them was the forest edge. Later, I studied applied ecology and conservation and realized that home, habitat or niche is an important factor for every species, including humans. Animal species can be negatively affected by exposure to the harshness of forest edges which include strong wind, direst sun shines, heat and other disturbances.

Habitat edges are a ubiquitous feature in the modern fragmented landscape (Ewers & Didham, 2008). Edges are found between blood cells (Lidicker, 1999), forest and rivers, forest and towns, mangrove, and the sea and also between forest and farmlands. Since Leopold (1933) introduced the notion of edge effects, many studies have been conducted to assess these aspects. I bring into the dialogue the status of l’Hoest’s monkeys on the edges of Bwindi Impenetrable National Park in Uganda. The premises of the study were from earlier findings that l’Hoest’s monkeys were more abundant at the edges than in the interior of Bwindi Impenetrable forest (Butynski, 1984; McNeilage et al., 2001). My approach was not to conduct another census, but to answer a few simple questions: Why? What are the advantages and disadvantages for l’Hoest’s monkeys being on forest edges? How frequently do l’Hoest’s monkeys leave the park to crop raid, and what kinds of conflicts are happening with local people when these monkeys are outside the park? I tested the dichotomy of edge effect theory by looking at (1) the characteristics and composition of l’Hoest’s monkeys’ habitat, (2) the distribution of food and disturbances and how they influence the behavioral ecology of the species, and (3) the conservation implications regarding the fate of l'Hoest's monkeys on the edges of Bwindi impenetrable forest.

Overall, the depth to which plant and food species distribution and diversity increase or decrease was estimated at 400m from the park boundary towards the forest interior. However, the depth of edge effects could vary depending on the variables considered. Edge effect depth usually follows a non-monotonic undulation or peak and tough patterns from the edge into the interior forest of Bwindi. Such patterns have also been reported in other studies (Rodrigues, 1998; Ewers & Didham, 2007; Bossart & Opuni-Frimpong, 2009). Broadbent et al. (2008) also demonstrated that edge effects influence species distribution and survival mostly in similar distances from the edge. They found that 54% of most depths of edge effects reported in the literature were between 100m and 2000m. The majority of effects however, could be localized between 200m and 400m (Olupot, 2004, Olupot & Chapman, 2006 and Olupot, 2009 for the Bwindi forest). The forest matrix also plays an important role in the ranging and survival of l'Hoest's monkeys. Half of the casualties that caused a decline in group size in the edge group of l'Hoest's monkeys happened in the matrix where monkeys were killed by farmers' dogs in retaliation for crop raiding.

Local people encroached regularly on the forest resources. They cut more poles for construction and also collected more firewood on the edge than in the interior forest. Cutting trees in the park is illegal. Nevertheless, Kayanja and Byarugaba (2001) believe that it is a common practice for local people in Uganda to encroach on state forest. In Bwindi, the only activity that was allowed in some parts of the study area was beekeeping.

Beekeepers from the local Kitojo community had the right to set their hives in the park from the edge to over 1000m. However, such a favor allowed irresponsible beekeepers to undertake illegal activities such as setting snares and collecting wood and cutting poles inside the park boundary. These activities had an impact on plant species distribution and survival at the park boundary. In the process of cutting a single pole many other species could be affected by trampling or even cutting.

The initial result of the activity budgets of the edge group revealed how l'Hoest's monkeys have adapted to living in that environment. When I evaluate demographic responses of the species to forest edges, I could not believe what I saw. The group size in both microhabitats has been declining over time. The edge and interior group sizes had declined by 22% and 11% respectively over a period of 1 year inside a national park. The large number of deaths resulted from forest edge disturbances. Eagle attacks and infanticide by solitary males happened on forest edges. No eagle kill or infanticide was recorded in the interior forest. The most unfortunate finding was that half of causalities (four out of eight) were of adult monkeys killed by farm guards while crop-raiding. If such edge threats continue to intensify in teh Bwindi forest, these numbers will become as alarming as for the case of Orang-utans in Indonesia whose population decreased by 30% over 10 years following logging activities (van Schaik, 2004).

Conserving for the future

I realized that border areas of forest reserves were population sinks due to strong edge effects, including conflict with humans (see Woodroffe & Ginsberg, 1998 for large carnivores). Human-induced activities contributed more to the extinction of species than stochastic processes. According to Woodroffe & Ginsberg (1998) conservation measures that aim only at combating stochastic processes are therefore unlikely to avert extinction. Instead, priority should be given to measures that seek to maximize reserve size or to mitigate species persecution on forest edges and in the matrix.

In this case, the l'Hoest's monkey has served as an ecological model system (Wolff et al., 1997) to be used in assessing several hypotheses regarding habitat loss, forest fragmentation, and edge effects. Forest edges can be ecological traps and population sink areas for certain species (Lehman et al., 2006a; Lehman et al. 2006b; Irwin, 2008). L'Hoest's monkeys are classified as a near-threatened species by IUCN (2008). With such an alarming decline, l'Hoest's monkeys may soon become endangered and ultimately extinct in the Bwindi forest. Therefore, intensive conservation work is needed, starting from bringing awareness to the local community about forest edge threats and teaching them how they should utilize as good shepherd the "multiple use zone" that have been allocated to them in the park. More resources are needed for mitigating the most obvious edge effect threat: human-wildlife conflict in Bwindi (Naughton-Treves, 1996; Baker, 2004; Andama, 2007). People need to be educated about which crop and where and when to plant species such as maize, sorghum, beans, peas, and potatoes, which attract primates outside the park. Such conservation outreach should target already established ecotourism groups around Bwindi to have a broader impact on the community as a whole.

Finally, I call for more comparative studies looking at microhabitat characteristics, species behavior, population dynamics, population genetics, and population health between groups of animal species found on the edge and in the interior of the forest. These studies will improve our knowledge regarding species natural history and support the continual efforts of park managers and conservationists in mitigating edge-related problems, including illegal plant collection, crop raiding, and species persecution in and around Bwindi Impenetrable National Park.

LITERATURE CITED

Andama E. 2007. *Invasive potential of Mauritius thorn (Cesalpinia decapetala) (Roth) Alston and its use to deter crop raiding by wild animals around Bwindi Impenetrable National Park, Uganda*. Dissertation. Makerere University.

Baker J. 2004. *Evaluating conservation policy: Integrated conservation and development in Bwindi Impenetrable National Park, Uganda*. Dissertation. University of Kent. UK.

Bossart J.L. & E. Opuni-Frimpong. 2009. Distance from edge determines fruit-feeding butterfly community diversity in Afrotropical forest fragments. *Environmenta Entomology* 38: 43-52.

Broadbent E.N., G.P Asner, M. Keller, D.E. Knapp, P.J.C. Oliveira & J.N. Silva. 2008. Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. *Biological Conservation* 141: 1745-1757.

Butynski T.M. 1984. *Ecological survey of the Impenetrable (Bwindi) forest, Uganda, and recommendations for its conservation and management*. New York Zoological Society. New York.

Ewers, R.M. & R.K. Didham. 2007. The effect of fragment shape and species’ sensitivity to habitat edges on animal population size. *Conservation Biology* 21: 926-936.

Ewers, R.M. & R.K. Didham. 2008. Pervasive impact of large-scale edge effects on a beetle community. *Proceedings of the National Academy of Sciences* 105, 5426–5429.

Irwin M.T. 2008. Diademed sifaka (*Propithecus diadema*) ranging and habitat use in continuous and fragmented forest: higher density but lower viability in fragments? *Biotropica* 40: 231-240.

IUCN 2008. *2008 IUCN Red List of Threatened Species*. www.iucnredlist.org. Downloaded on 20 February 2009.

Kayanja F. I. B. & D. Byarugaba. 2001. Disappearing forests of Uganda: The way forward. *Current Science* 81: 936-947.

Lehman S.M., A. Rajaonson & S. Day. 2006a. Lemur responses to edge effects in the Vohobola III classified forest, Madagascar. *American Journal of Physical Anthroplogy* 68: 293-299.

Lehman, S. M., A. Rajoanson, & S. Day 2006b. Edge effects and their influence on lemur distribution and density in southeast Madagascar. *American Journal of Physical Anthropology* 129: 232–241.

Leopold A. 1933. *Game management*. Charles Scribner's Sons. New York.

Lidicker W.Z. 1999. Responses of mammals to habitat edges: an overview. *Landscape Ecology* 14: 333-343.

McNeilage A., A.J. Plumptre, A. Brock-Doyle & A. Vedder. 2001. Bwindi Impenetrable National Park, Uganda: Gorilla census 1997. *Oryx* 35: 39-47.

Naughton-Treves L. 1996. *Uneasy neighbours: Wildlife and farmers around Kibale National Park*. Dissertation. University of Florida. Gainesville.

Olupot, W. 2004. *Boundary edge effects in Bwindi Impenetrable National Park*. Institute of Tropical Forest Conservation. Uganda. Pp 127-186.

Olupot W., C.A. Chapman. 2006. *Human encroachment and vegetation change in isolated forest reserves: the case of Bwindi Impenetrable National Park, Uganda*. In: Laurance, W.F. & C.A. Peres (Eds.). *Emerging Threats to Tropical Forests*. The University of Chicago Press. Chicago. Pp. 127-142.

Olupot W. 2009. A variable edge effect on trees of Bwindi Impenetrable National Park, Uganda, and its bearing on measurement parameters. *Biological Conservation* 142: 789-797.

Rodrigues E. 1998. *Edge effects on the regeneration of forest fragments in south Brazil*. Dissertation. Harvard University.

van Schaik C. 2004. *Among orangutans: red apes and the rise of human culture*. Belknap Press of Harvard University Press. Cambridge. Massachusetts.

Wolff J.O., E.M. Edge & W.D. Schauber. 1997. Effect of habitat loss and fragmentation on behavior and demography of Gray-tailed voles. *Conservation Biology* 11: 945-956.

Woodroffe R. & J.R. Ginsberg. 1998. Edge effects and extinction of populations inside protected areas. *Science* 280: 2126-2128.