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The Ecology and Conservation of the Critically Endangered Cross River Gorilla in Cameroon

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By

Sarah Cahill Sawyer

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ABSTRACT:

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The Cross River gorilla (*Gorilla gorilla diehli;* hereafter: CRG) is one of the world's most endangered and least studied primates. CRG exist only in a patchy distribution in the southern portion of the Cameroon-Nigeria border region and may have as few as 300 individuals remaining, divided into 14 fragmented subpopulations. Though Western gorillas (*Gorilla gorilla* spp) probably once inhabited much greater ranges throughout West Africa, today CRG represent the most northern and western distribution of all gorillas and are isolated from Western lowland gorilla populations by more than 250 km. CRG have proved challenging to study and protect, and many of the remaining subpopulations currently exist outside of protected areas. Very little is known about where the various subpopulations range on the landscape or why they occur in a patchy distribution within seemingly intact habitat. Active efforts are currently underway to identify critical habitat for landscape conservation efforts to protect the CRG in this biodiversity hotspot but, to date, a lack of understanding of the relationship between CRG ecology and available habitat has hampered conservation endeavors. This dissertation aims to improve our understanding of CRG ecology and distribution to inform conservation management decision making.

This research has four main components. First, I describe the plant diet of one CRG subpopulation (the Mone subpopulation). Successful habitat management for primate conservation requires understanding which plants are important and how these plants vary in availability across the landscape. Using feeding trail sign collected over a 10 month period, I record the components of the CRG diet, evaluate CRG selectivity among herbaceous food species, compare Mone CRG diet to that of another CRG subpopulation, and examine differences in herbaceous food availability in areas used and unused by the CRG. During the study period, the CRG ate 141 different plant parts from 102 different species, 23 of which were quantitatively important in the diet. Similarly to other Western lowland and CRG populations, *Landolphia*, *Aframomum,* and *Palisota spp*, were important staple species for the Mone CRG and *Marantochloa purpurea* played an important fallback role in their diet. By contrast, *Araceae* species, like *Cercestis camerunensis*, may be more important to the CRG at Mone than elsewhere. My results suggest that CRG in the Mone-

Mt. Oko region prefer certain foods in their diet, and may also selectively use areas with higher availability of preferred foods.

Second, I estimate the Mone subpopulation range and assess both the effects of model choice on resulting range estimates and the conservation utility of various models. Measuring and characterizing the area utilized by a population or species is essential for evaluation of conservation status and for effective allocation of habitat to ensure population persistence. Models considered in this study range from basic traditional approaches (e.g. Minimum Convex Polygon) to newer home range techniques such as Local Convex Hull (LoCoH). I used overlap analysis comparing sub-sampled to complete data sets to evaluate the robustness of various modeling techniques to data limitations. I employed Likelihood Cross Validation Criterion to compare core range model performance. Results suggest that differing LoCoH models produce similar range estimates, are robust to data requirements, provide a good fit for core habitat estimation, and are best able to detect unused habitat within the subpopulation range. LoCoH methods may thus be useful for studies of habitat selection and factors limiting endangered species distributions. However, LoCoH models tend to overfit data, and Kernel methods may provide similar information about animal space use while supporting protection of larger swaths of critical habitat. Subpopulation range analyses for conservation/management planning should therefore explore multiple modeling techniques, and employ both qualitative and quantitative assessments to select the best models to inform decision making for species of conservation concern.

Third, I review current use of Least Cost Path modeling techniques for connectivity conservation, and highlight both weaknesses and ways to improve application for species like the Cross River gorilla. Promoting connectivity between areas utilized by isolated subpopulations is essential to maintain population viability in fragmented species like the CRG, where each subpopulation contains relatively few individuals. The most common approach to connectivity design is the Least Cost Path (LCP) analysis, which has been applied to the CRG landscape. This review highlights three weaknesses common in recent LCP analyses. First, LCP models typically rely on remotely-sensed habitat maps, but few studies assess whether such maps are suitable proxies for factors affecting animal movement or consider the effects of adjacent habitats. Secondly, many studies use expert opinion to assign costs associated with landscape features, yet few validate these costs with empirical data or assess model sensitivity to errors in cost assignment. Thirdly, studies that consider multiple, alternative movement paths often propose width or length requirements for linkages without justification. LCP modelling and similar approaches to linkage design guide connectivity planning, yet often lack a biological or empirical foundation. Ecologists must clarify the biological processes on which resistance values are based, explicitly justify cost schemes and scale (grain) of analysis, evaluate the effects of landscape context and sensitivity to cost schemes, and strive to optimize cost schemes with empirical data. Research relating species' fine-grain habitat use to movement across broad extents is desperately needed, as are methods to determine biologically relevant length and width restrictions for linkages. While data on such fine grain habitat use have to date been lacking for the Cross River gorilla, this dissertation research aims to improve our understanding of these variables.

Thus, finally, I use hierarchical resource selection functions (RSFs) to examine habitat selection and requirements of the CRG at multiple scales to inform connectivity modeling and conservation planning. Specifically, I employ generalized additive models at the scale of the subpopulation range and conditional logistic regression at the scale of individual movements. Understanding resource and habitat selection by endangered species will better inform conservation planning for protection of both critical habitat, and essential linkages between subpopulations. Results indicate that CRG habitat selection is highly scale dependent. Localized measures of habitat quality strongly influenced selection at the subpopulation or landscape scale, while human activity and food availability are the best predictors of selection at finer scales. Understanding why CRG do not occur in seemingly suitable habitat is crucial for designating critical habitat both within and between CRG subpopulations. My results indicate that conservation planning to maintain critical habitat and connectivity among CRG populations will require an integrative, multi-scale planning approach incorporating large-scale landscape characteristics, human use patterns and CRG food availability. Further fine-scale data collection across the landscape will be necessary to use RSF results in connectivity models to inform conservation of important linkages between subpopulations.

This research marks a significant addition to the current limited knowledge about the CRG dietary and spatial ecology and conservation biology. My study results complement past and ongoing research by other PhD students, conservation NGOs, and government officials, and compiling these various works will likely provide us with a more complete understanding of CRG ecology for effective conservation decision making

This dissertation is dedicated to the memory of Dr. Ymke Warren. Ymke acted as a guide and mentor throughout the study, and lost her life too soon to see her great impact, an impact that reaches far beyond the scientific scope of this study.

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Chapter 1
General Introduction

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Sawyer, J. & Sawyer, S. (2011) Lessons from the Mist: What can international environmental law learn from gorilla conservation efforts? *Georgetown International Environmental Law Review*, **Volume XXIII**, Issue 3, 365-396. Copyright © 2011, Jessica Sawyer and Sarah Sawyer.

Introduction

Despite worldwide focus on the threat of extinction and the importance of conservation, biodiversity remains on the decline. The earth has lost a third of its vertebrate populations in the past forty years, is in danger of losing a quarter of its plant species and humanity has developed a footprint that long since exceeded the sustainable biological capacity of the planet (Secretariat of the Convention on Biological Diversity 2010). At the same time, three billion people live on less than $2.50 a day, and more than 80% of the world's population resides in countries where income differentials are widening (Shah, 2010). In 2002, the parties to the U.N. Convention on Biological Diversity met and agreed to work together "to achieve by 2010 a significant reduction of the current rate of biodiversity loss at the global, regional and national levels as a contribution to poverty alleviation and to the benefit of all life on Earth" (Secretariat of the Convention on Biological Diversity 2010). Eight years later, the parties conceded that this goal had not been met (Secretariat of the Convention on Biological Diversity 2010). It is clear that successful conservation endeavors will require not only additional resources, such as human and financial capital, legal enforcement frameworks, and multilateral agreements, but also additional ecological knowledge about the species at risk.

Many conservation projects begin with a single animal or plant that captures the attention of the local or international community. With this international attention often comes a call for conservation efforts. When asking local communities or the world at large to make changes that may be unpopular, it is advantageous to ensure that the biodiversity outcomes are as visible as possible. Some of the most visible outcomes can be achieved for charismatic megafauna, or flagship species. Flagship species have been variably defined as: 1) popular charismatic species that serve to rally support and encourage public awareness, interest, and sympathy; 2) species that draw financial support for conservation; and 3) species that become symbols and leading elements of ecosystem protection campaigns (Caro et al. 2004). Though flagship species are now considered ecologically poor surrogates for the protection of other species, political and social realities may mean that conservation must depend on flagship species for financial and public support (Williams et al. 2000). The promotion of particular charismatic and threatened species can increase total conservation funding available and draw attention to threatened areas and particular communities (Tisdell 2006).

This research focuses on gorillas, which are among the most recognizably threatened species in the world, and are the subject of several long-term conservation efforts in their native habitats. Gorillas are well placed to serve as conservation flagship species, as they have captured the hearts and minds of the public (Weber & Vedder 2001). They are very close to humans in both appearance and behavior, exhibiting strong mother-infant bonds, recognizable affiliative and aggressive interactions between group members, and a strong dependence on learning in the early life stages. Diane Fossey established the first gorilla research station, Karisoke, over 40 years ago, in September 1967, and gorillas have been consistently studied ever since (Stewart et al. 2001). Compared with other primates, gorillas have long been part of the public consciousness, particularly since the 1980s, when "Gorillas in the Mist" became successful worldwide through both book and film (Weber & Vedder 2001). Regular censuses have been carried out since George Schaller's first Virunga census in the 1960s, showing the decline of gorilla populations as their habitats have been eroded in the 1960s, 70s, and 80s, and then slight growth as research, conservation projects, and tourism took root (Stewart et al. 2001). Public willingness to donate funds to conserve species increases with knowledge of the species conservation status; gorillas are visibly endangered (Tisdell 2006). In fact, gorillas were the main reason for the creation of the first African National Park: Albert National Park, gazetted in 1926 (Stewart et al. 2001). Aside from their potential conservation benefits, gorillas are threatened throughout much of their range (Caldecott & Ferriss 2005; Rothman et al., 2006, IUCN, 2001) and implementation of efficient habitat conservation for the persistence of gorilla species requires reliable data on the ecology of the taxa, as well as the threats it faces.

Gorillas: Biology and Limiting Factors

There are two species of gorilla currently recognized, each containing two subspecies. Eastern gorillas consist of Eastern lowland gorillas (*Gorilla beringei graueri*) and Mountain gorillas (*Gorilla beringei beringei*). Western gorillas consist of Western lowland gorillas (*Gorilla gorilla gorilla*) and Cross River gorillas (*Gorilla gorilla diehli*) (Caldecott & Ferriss 2005). Likely less than 700 Mountain gorillas exist today and they are found in only two populations, located in Uganda, Rwanda, and the Democratic Republic of Congo (Ferriss et al. 2005). Less than 300 Cross River gorillas exist today, and are located in an estimated 14 isolated subpopulations found only in Cameroon and Nigeria (Oates et al 2003). Cross River and Mountain gorillas are listed as two of the world's twenty-five most endangered primate taxa (Caldecott & Ferriss 2005).

Demographic rates and area requirements of gorillas interact with other limiting factors, such as human and natural disturbances, to limit population sizes. Gorillas are a relatively long-lived, large-bodied, K-selected species, with low reproductive rates and high levels of infant dependency (Ross 1992). Adult female Western gorillas weigh about seventy-two kilograms, and males may weigh up to twice as much (Smith & Jungers 1997). Large bodies often both demand large home ranges to fulfill caloric requirements and entail long developmental/growth phases, thereby limiting abundance in multiple ways. Gorillas are social animals, living in groups ranging from two to over thirty individuals. Large groups require larger home ranges to sustain their energetic demands, making animals more conspicuous, and therefore more vulnerable to hunters. Gorilla home range sizes vary from three to forty square kilometers - often larger than available habitat fragments - which prevent them from surviving or colonizing in highly fragmented ecosystems (Robbins & McNeilage 2003).

In addition to large area requirements, long-lived, large-bodied species often have low reproductive rates. Gorilla inter-birth intervals range from four to six years, infant mortality ranges from 8 to 42%, and reproductive rates fall between 0.18 and 0.23 births per adult female per year (Robbins et al. 2004; Robbins & Robbins 2004). Low reproductive rates prevent gorillas from recovering quickly following discrete disturbances or continuous stressors. High infant dependency magnifies hunting impacts by coupling mortality of infants under the age of three to the loss of their mothers. When combined, low demographic rates, large area requirements, and particular vulnerability to anthropogenic stressors likely limit gorillas to existence at low and therefore vulnerable population densities. More specific external threats to gorilla species vary by population and location, but all gorilla subspecies are arguably in need of protection.

The Cross River gorilla: Natural History, Threats, and Conservation Actions

The Cross River gorilla (*Gorilla gorilla diehli*) is one of Africa's most endangered, yet least studied, primates (Bergl & Vigilant 2007; Oates et al. 2003). The Cross River gorilla (hereafter CRG) is a subspecies of Western gorilla (*Gorilla gorilla*) inhabiting the border regions of Cameroon and Nigeria, and is the most northern and western of all gorilla populations. Though the subspecies is likely to have historically occurred in high numbers over a continuous distribution, current studies estimate that only 250 to 350 individuals remain divided into approximately 14 subpopulations (Bergl 2006; Bergl et al. 2011; Oates et al. 2003). Difficult terrain, historical over-hunting by human populations, and the trans-national distribution of the subpopulations make the Cross River gorilla difficult to study and protect. In addition, many subpopulations currently fall outside of protected areas. Limited available data suggest that the subspecies population is both small and declining. Threats to CRG include continued habitat destruction, fragmentation, logging, and hunting (Oates et al. 2003).

Historical Distribution and Population Isolation:

Historical isolation and selective pressures likely drove the evolutionary separation of the Cross River gorillas from other Western gorillas by allopatric differentiation, and continue to influence CRG distribution and abundance today. Large scale historical processes and climate patterns that affected the entire continent of Africa have played key roles in determining primate distributions. Repeated expansions and contractions of forested regions over glacial/interglacial time scales have led to a fragmented pattern of persisting forest habitats (Chapman et al 2006). In addition, unlike other continents where primates exist, Africa has a dry climate and most of the rainforest is restricted to a narrow tropical range. Accordingly, African primates tend to occur in relatively small forest or savannah blocks and occupy small geographic ranges (Chapman 2006). These historic and evolutionary processes greatly influence current CRG distribution and abundance by limiting both colonization (e.g. by fragmentation/isolation of suitable habitat) and survival (e.g. by unsuitability of habitat outside of tropical regions) mechanisms throughout equatorial Africa.

Though Western gorillas probably once inhabited much greater ranges throughout West Africa, the CRG have today the most northern and western distribution of all gorillas and are isolated from the other West African gorilla populations by substantial distances (Sarmiento & Oates 2000). The closest living gorilla populations occur approximately 260 kilometers from the CRG. Isolation likely arose gradually through a combination of factors including the Sanaga River's division of the region, the presence of grasslands and fragmented forests throughout the Cameroon highlands, and the expansion and intensification of human settlements in the lowlands of Western Cameroon (Sarmiento & Oates 2000). These ultimate factors continue to limit the large-scale geographic distribution and abundance of CRG. However, proximate factors, such as relative food abundance and anthropogenic impacts, clearly play a more important role in the smaller-scale patchy distribution of CRG we see today.

Distribution of Food Species:

Food is an important and common limiting factor to species' abundance and distribution. Many primate populations have been observed to decline significantly when important food species are selectively removed through logging or other processes (Chapman et al 2006). Recent studies examining gorilla distributions indicate that western gorillas occur at higher densities in areas where their staple foods are most abundant (Rogers et al 2004), and that food availability has important implications for population dynamics, including setting carrying capacity limits (Nkurunungi et al 2004). The distribution and relative abundance of resources likely influences many aspects of gorilla sociality and ranging patterns (Doran & McNeilage 2001), particularly when they are dependent on rich, dense food species distributed patchily in time or space.

CRG are selective frugivore-folivores and, therefore, habitat type, density of terrestrial herbaceous vegetation, and presence of important fruit species all interact to potentially limit species distribution and abundance. Because frugivores and omnivores require more area per unit biomass than other species (Godfrey & Irwin 2007), CRG numbers are limited by their dietary requirements and subsequent area requirements.

They will also be limited by the phenology and seasonality of fruit species, and may shift their ranging patterns in response to these patterns. Despite these general patterns, preliminary data indicate that human land-use, rather than food availability, acts as the force driving CRG habitat selectivity (Sunderland-Groves 2008) and distribution.

Human Impacts:

One important human factor, land-use and land-cover change, has led to habitat fragmentation in the Takamanda-Mone landscape and Cross River regions of Cameroon and Nigeria. Habitat fragmentation, generally caused when humans clear native vegetation to meet the needs of growing populations, expanding both food and shelter uses of nearby land, is a major contributor to the current mass extinction crisis (Swart and Lawes 1996; Brooks et al 2002; Hilty et al 2006; Anderson & Jenkins 2006) and poses a particularly serious danger to small populations (Fahrig & Merriam 1994) like the CRG. By dividing animal populations into isolated habitats, fragmentation increases species' risk of extinction from inbreeding and stochastic effects, and limits the ability of populations to move in response to short-term perturbations (e.g. harvest, habitat degradation) and long-term threats (e.g. climate change). Habitat fragmentation may therefore significantly limit CRG distribution and abundance, as well as viability, by isolating subpopulations. The current patchy distribution of CRG into 14 subpopulations may be a consequence of habitat fragmentation for agriculture and human development. Studies estimate that forested areas available to individual subpopulations range from only four to thirty-five square kilometers (Oates el al 2003).

Logging presents another major threat to CRG habitat. One-hundred seventy thousand square kilometers of Cameroon's forests had already been either logged or allocated for logging concessions by the year 2000 (Ferriss 2005). Forest products represent over 10% of all trade in Cameroon; previously untouched CRG habitats are now on the table for proposed logging concessions (pers comm. with NGO staff). However, habitat fragmentation is not the only impact of logging on wild animals. Logging also increases the hunting threat to animals, through two major mechanisms: (1) logging roads increase access to remote areas for hunting and other forms of exploitation, and (2) by importing a labor force with purchasing power, logging can increase demand for wild-caught meat.

Cross River gorillas, like many wildlife species worldwide, are jeopardized by hunting (Robinson et al 1999, Wilkie & Carpenter 1999). Hunting directly impacts species' abundances by removing individual organisms, and can have an indirect impact on abundance by raising stress levels, changing behaviors, and reducing organisms' reproductive output (Pauli & Buskirk 2007). CRG are hunted for meat and body parts. Limited harvest studies indicate that one to three CRG individuals are killed by hunters annually, and this is likely an underestimation of CRG hunting. Hunting of other species is common in the area, which may indirectly affect CRG through stress and behavioral responses, habitat modifications, or disease transmission from hunters. While hunting gorillas is illegal in Cameroon, environmental laws are rarely, if ever, enforced at any level of the legal or judicial system. Therefore, hunting has both direct and indirect impacts on CRG abundance.

Hunting may also significantly limit CRG distribution. Prior to this study, presence of gorilla sign has been found to be negatively correlated with human hunting sign, and positively correlated with steepness of slope (Sunderland-Groves 2008), indicating an avoidance of human contact. Significant differences of slope and elevation have been recorded between CRG and human village locations and CRG distribution may currently be limited to steep, remote locations inhospitable to humans. Groves (2002) reported that these gorillas were only found to exist within higher altitude, difficult to access areas where hunting pressure was found to be less intensive compared to lowland areas. Therefore, the existence of the CRG in a disjointed distribution in seemingly intact habitat, may be a result of hunting pressure and other human-utilization patterns.

Cross River gorilla *Conservation in Cameroon*

This research was carried out in Cameroon, home to more than half of the known CRG population. Cameroon has the judicial and ministerial power to protect Cross River gorillas, at least on paper, but lacks the resources and transparency to take effective action. Law No. 94/01 (1994) sets out Cameroon's forestry, wildlife, and fishery regulations (Forboseh et al. 2007; Ngalla et al. 2005). According to the law, gorillas are listed as category A species, which are completely protected against hunting, capture, and sale. Additionally, protected areas aimed at both species and habitat conservation can be established by the Ministry of Forestry and Wildlife (MINFOF), which is charged with preserving the country's biodiversity (Ngalla et al. 2005).

Significant obstacles to success hamper CRG conservation in Cameroon. Economic, educational, and cultural divides impede effective communication across the local, national, and international levels of CRG conservation efforts. The economic interests of locals seem to promote unsustainable use of natural resources and discourage participation in conservation endeavors (pers comm. with local hunters). Local cultural values and expectations have not been adequately addressed in regional conservation endeavors, and local understanding of the ultimate goals, costs, and benefits of these programs is low. Consistent and sustainable enforcement measures are lacking in the current program. Local government presence in rural areas, where enforcement of international legislation is most needed, is almost nonexistent. Locals are often unaware they are conducting illegal activities (e.g., hunting dwarf crocodiles, preventing non-locals from entering governmentally owned forest, etc.) (pers comm. with local hunters). These gaps in education, communication, and consistent enforcement continue to cause conflict between local populations and the researchers and management of national parks.

Another obstacle is the lack of consistent, sustainable sources of funding for conservation programs, and local governmental capacity or willingness to enforce conservation laws remains low (pers comm. with local villagers). In addition to grants from the Global Environment Facility (GEF), Cameroon requires a constant influx of funding to develop working conservation programs. In order for bans on hunting and trade to be enforced, or for logging proposals to be denied in favor of conservation or protected area establishment, the benefits of conservation must outweigh its costs. Salaries of those employed in conservation must be consistently greater than potential payout from activities negatively impacting listed species (e.g., hunting) and/or governments must benefit from protecting biologically valuable areas (Kassenoff 1999; Kohn & Ives 2007). However, in many villages in the CRG landscape, a hunter can kill five porcupines or more in a single evening, for revenues totaling up to three times those of even a generous research/conservation salary (pers obs). Additionally, the opportunity cost of the government refraining from logging an area in Cameroon has been estimated at US $15,000 per square kilometer per year, making additional logging opportunities hard to pass up (Varty et al. 2005).

From 1993 to 2003, the Ministry of Environment and Forestry (now the Ministry of Forestry and Wildlife) used over US $12 million in an effort to gazette seven parks, create development plans, and rehabilitate the Cameroon National Herbarium (Global Environment Facility 2010). In a country where the Gross National Income per person in 2002 was US $560, conservation of species like Cross River gorillas needs to begin to pay for itself in order for international legislation to have any hope of implementation (Ngalla et al. 2005). While many countries in similar situations draw conservation funds from ecotourism, Cameroon's lack of necessary infrastructure and inability to take advantage of the ever-growing African ecotourism market prevent such a solution. The GEF stated that in Cameroon "sustainable sources of funding must be secured in order to strengthen the local organizations, provide adequate compensation for the sacrifices made by local populations for biodiversity conservation, and to sustain community-based development" (Ngalla et al. 2005) Without continued and sustainable sources of funding, legislation is powerless.

Despite the many obstacles, progress is being made in Cameroon toward positive, tangible conservation outcomes. A series of joint projects between the Ministry of Forests and Wildlife (MINFOF), Wildlife Conservation Society (WCS), German Technical Corporation (GTZ), German Development Service (DED), and World Wildlife Fund (WWF) are currently trying to make real progress toward CRG conservation (Science Daily 2008). They recently succeeded in establishing the Kagwene Gorilla Sanctuary where research assistants from local villages are employed and ecological data collection and capacity building are carried out. They also gazetted Takamanda National Park in 2008, to form a contiguous protected area with the Nigerian Cross River National Park. While this conservation progress looks promising, these endeavors are still threatened by funding issues, socio-political miscommunications, and discrepancies in priorities. Placement of the Takamanda park headquarters has sparked local community tribal disagreements and has led to community refusal to cooperate with government and NGO conservation measures (pers obs). Additionally, despite the government's 2002 Plan de Zonage recommendation that the Mone Forest Reserve be upgraded to a Wildlife Sanctuary, a lack of funding options has recently sparked discussions to open the Reserve as a logging concession (Forboseh et al. 2007; pers obs).

Recent conservation progress addressing issues of international funding, local economic needs, and capacity building may indicate that Cameroon is trying to get on the path to successful CRG conservation. Kassenoff noted that "CITES should institute paid programs whereby citizens who are familiar with the surrounding ecosystem are paid to monitor and protect the endangered species specified within the treaty (Kassenoff 1999)." WCS Cameroon has recently instated a "Gorilla Guardian" program which fits precisely this prescription. Additionally, DED and GTZ are placing emphasis on sustainable use of natural resources and alternative income projects, including bee-keeping, snail farming, and cassava plantations (Nuesiri & Fombad 2006). The NGOs encourage local communities to support conservation legislation by providing viable alternatives to breaking the law. GTZ is working to increase local enforcement capacity by spearheading the implementation of "Forest Law Enforcement, Governance and Trade" in Cameroon (German Technical Corporation 2010). This includes, among other initiatives, a national monitoring strategy to combat the illegal timber trade (German Technical Corporation 2010). Finally, funding from the German Development Bank (KFW) and the U.S. Fish and Wildlife Service administered Great Apes Conservation Fund may provide the necessary international support to promote national legislative implementation and enforcement (Science Daily 2008). Progress towards CRG conservation is being made on the Nigerian side as well. Nigeria shares many of the same conservation challenges as Cameroon, but faces additional challenges as well – including higher human population densities and increased land-cover conversion. Therefore, Nigerian conservation priorities include improving protected area management and infrastructure, establishment of buffer zones corridors between and around existing protected areas, increased conservation education, and, like Cameroon, additional research into the CRG ecology (Oates et al. 2007).

Cross River gorilla conservation is in the very early stages of implementation. Success will require the continued efforts of the Cameroonian government, national and international NGOs, and most importantly, the local communities. Without increased commitment and capacity building, success will be difficult to achieve. In addition, data on the ecology of the CRG are scarce, and research must be carried out to inform effective conservation decision making. Elucidation of factors influencing CRG distribution and abundance will be critical for conservation of connectivity and viable population sizes throughout the CRG range. Difficult terrain, historical over-hunting by human populations, and the trans-national distribution of the subpopulations make the Cross River gorilla very difficult to study, and relatively few studies on the subspecies have been conducted to date (but see Groves 2002; Oates et al 2003; Bergl & Vigilant 2006). Reports suggest that predicting suitable habitat may be critical for conservation and future survival of the CRG (Sunderland-Groves 2008). This dissertation research aims to improve our understanding of CRG ecology and distribution to inform conservation management decision making. It marks a significant addition to the current limited knowledge about the CRG dietary and spatial ecology and conservation biology.

Dissertation Overview

In the second chapter, I describe the diet of the Cross River gorilla (CRG), to inform conservation decision-making and augment our understanding of great ape feeding ecology. Over a 10 month period, I observed feeding-trail remains of the Mone-Mt. Oko CRG subpopulation and measured herbaceous stem densities within their range. Using these data, I compiled a list of food species in the diet, determined important staple, seasonal, and fallback foods, and measured relative preference and availability of herbaceous species eaten. During the study period, the CRG ate 141 different plant parts from 102 different species, 23 of which were important in the diet. Similarly to other Western lowland and CRG populations, *Landolphia*, *Aframomum,* and *Palisota spp*, are important staple species for the Mone CRG and *Marantochloa purpurea* plays an important fallback role in their diet. On the other hand, Araceae species, like *Cercestis camerunensis*, may be more important to the Mone CRG than has been observed elsewhere. My results suggest that CRG in the Mone-Mt. Oko region show preference for certain foods in their diet, and may also select their ranging habitat for areas with higher availability of preferred foods.

In chapter three I assess the effect of home range model choice on subpopulation range estimation for the Cross River gorilla, and evaluate the conservation conclusions that can be drawn from each model. Models considered range from basic traditional approaches (e.g. Minimum Convex Polygon (MCP)) to newer home range techniques such as Local Convex Hull (LoCoH). Overlap analysis comparing sub-sampled to complete data sets are used to evaluate the robustness of various modeling techniques to data limitations. Likelihood Cross Validation Criterion is employed to compare core range model performance. Results suggest that differing LoCoH models produce similar range estimates, are robust to data requirements, provide a good fit for core habitat estimation, and are best able to detect unused habitat within the subpopulation range. LoCoH methods may thus be useful for studies into habitat selection and factors limiting endangered species distributions. However, LoCoH models tend to trace data too tightly (overfit), and Kernel methods may provide similar information about animal space use while supporting protection of larger swaths of critical habitat. Subpopulation range analyses for conservation/management planning should therefore explore multiple modeling techniques, and employ both qualitative and quantitative assessments to select the best models to inform decision making for species of conservation concern.

In chapter four, I explore the most popular method used to inform habitat linkage design for patchily distributed species like the CRG, namely least-cost path (LCP) analysis. LCP designates a landscape resistance surface based on hypothetical ‘costs’ that landscape components impose on species movement, and identifies paths that minimize cumulative costs between locations. While LCP analysis represents a valuable method for conservation planning, its current application has several weaknesses. Here, I review LCP analysis and identify shortcomings of its current application that decrease biological relevance and conservation utility. I examine trends in published LCP analyses, demonstrate the implications of methodological choices with my own LCP analysis for bighorn sheep *Ovis canadensis nelsoni*, and point to future directions in cost-modelling. This review highlights three weaknesses common in recent LCP analyses. First, LCP models typically rely on remotely-sensed habitat maps, but few studies assess whether such maps are suitable proxies for factors affecting animal movement or consider the effects of adjacent habitats. Secondly, many studies use expert opinion to assign costs associated with landscape features, yet few validate these costs with empirical data or assess model sensitivity to errors in cost assignment. Thirdly, studies that consider multiple, alternative movement paths often propose width or length requirements for linkages without justification. LCP modelling and similar approaches to linkage design guide connectivity planning, yet often lack a biological or empirical foundation. Ecologists must clarify the biological processes on which resistance values are based, explicitly justify cost schemes and scale (grain) of analysis, evaluate the effects of landscape context and sensitivity to cost schemes, and strive to optimize cost schemes with empirical data. Research relating species' fine-grain habitat use to movement across broad extents is desperately needed, as are methods to determine biologically relevant length and width restrictions for linkages. While data on such fine grain habitat use have to date been lacking for the Cross River gorilla, this dissertation research aims to improve our understanding of these patterns.

Thus, in chapter five, I use hierarchical resource selection functions to refine our understanding of CRG habitat use at multiple spatial scales. Specifically, I employed generalized additive models at the scale of the subpopulation range and conditional logistic regression at the scale of individual movements. My results suggest that CRG habitat selection is highly scale dependent. Localized measures of habitat quality strongly influenced selection at the subpopulation or landscape scale, while human activity and food availability were the best predictors of selection at finer scales. Conservation planning to maintain critical habitat and connectivity among CRG populations will require an integrative, multi-scale planning approach incorporating large-scale landscape characteristics, human use patterns, and CRG food availability.

In the final chapter of this dissertation, I draw general conclusions and make recommendations for future ecological research and conservation endeavors to better understand and protect the Cross River gorilla.

CHAPTER 2:

Feeding Ecology of the Cross River Gorilla: A Preliminary Diet Assessment of the Mone Subpopulation

Abstract

Diet and food availability have important implications for the ecology and conservation of endangered primates. Successful habitat management for primate conservation requires understanding which plants are important and how these plants vary in availability across the landscape. Here, I describe the plant diet of the least studied and most endangered of the great apes, the Cross River gorilla (*Gorilla gorilla diehli;* hereafter CRG), to inform conservation decision-making and augment our understanding of great ape feeding ecology. Over a 10 month period, I observed feeding-trail remains of the Mone-Mt. Oko CRG subpopulation and measured herbaceous stem densities within their range. Using these data, I compiled a list of food species in the diet, determined important staple, seasonal, and fallback foods, and measured relative preference and availability of herbaceous species eaten. During the study period, the CRG ate 141 plant parts from 102 different species, 23 of which were quantitatively important in the diet. Similarly to other Western lowland and CRG populations, *Landolphia*, *Aframomum, and Palisota spp*, were important staple species for the Mone CRG and *Marantochloa purpurea* played an important fallback role in their diet. By contrast, Araceae species, like *Cercestis camerunensis*, may be more important to the CRG at Mone than elsewhere. Our results suggest that CRG in the Mone-Mt. Oko region prefer certain foods in their diet, and may also selectively use areas with higher availability of preferred foods. While research on CRG has, to date, emphasized the conservation value of steep, high elevation, inaccessible sites, this study highlights the need also to include flatter, lower elevation regions which may contain higher staple food availability.

Key Words: Food Preferences, Diet, Feeding Ecology, Cross River gorilla, Conservation Planning

Introduction

Diet and resource availability not only shape the anatomy and socioecology of primates, but also directly limit their distributions, population densities, and reproductive success (Altmann, 1991, 1998; Byrne *et al.*, 1993; Johns & Skorupa, 1987; Marshall *et al.*, 2009; Williamson *et al.*, 1990; Wrangham, 1979). Thus, variation in feeding ecology has important implications for behavioral and ecological theory, as well as conservation management applications. Understanding diet is particularly important for highly endangered primate species (Fan *et al.*, 2011; McNeilage 2001; Rothman *et al.*, 2006). Conservation management will more likely be successful where we can identify important food plants, determine their role in habitat carrying capacity for a species, and use their distribution to prioritize habitats for conservation action (McNeilage, 1995; Rogers *et al.*, 2004; Rothman *et al.*, 2006).

The genus *Gorilla* is threatened throughout much of its range (Caldecott & Ferriss 2005; Rothman *et al.*, 2006, IUCN, 2001) and implementation of efficient habitat conservation for the persistence of gorilla species draws upon dietary and ecological data. Gorillas exist in diverse ecological conditions with various resource availabilities (Doran-Sheehy *et al.*, 2004; Masi *et al.*, 2009; Robbins *et al.*, 2006). Studies in Rwanda (e.g. McNeilage 2001; Vedder 1984; Watts 1984), Uganda (e.g. Ganas *et al.*, 2004, Robbins *et al.*, 2006, Rothman *et al.*, 2007), Gabon (e.g. Head *et al.*, 2011), and Central African Republic (e.g. Doran-Sheehy *et al.*, 2006; Masi *et al.*, 2009; Remis 2003) indicate dramatic dietary variation across regions and both species, largely reflecting different ecological circumstances (Robbins *et al.*, 2006; Masi *et al.*, 2009). Such variation highlights the value of dietary and ecological data for poorly studied subspecies in need of conservation management. Increasing our knowledge of such poorly studied groups will facilitate not only better conservation strategizing, but also greater understanding of resource partitioning, niche separation, and ecological evolution among primates (Doran-Sheehy *et al.*, 2009; Robbins *et al.*, 2006; Tutin *et al.*, 1997).

Patterns that could aid in predicting dietary differences across gorilla subspecies are evident in existing data for the two gorilla species, Eastern gorillas (subspecies: Mountain gorilla- *Gorilla beringei beringei* and Eastern lowland or Grauer's gorilla- *Gorilla beringei graueri*) and Western gorillas (subspecies: Western lowland gorilla-*Gorilla gorilla gorilla* and Cross River gorilla – *Gorilla gorilla diehli*). Eastern gorillas, particularly Mountain gorillas, appear to be relatively more specialized terrestrial folivores at higher elevation sites where fruit is less available, showing increased dietary variability and frugivory with increasing fruit availability at lower-elevation sites (Ganas *et al.*, 2004; McNeilage 2001; Robbins *et al.*, 2006; Rothman 2006; Rothman *et al.*, 2007; Vedder 1984; Watts 1984). Grauer's gorilla populations inhabiting intermediate elevations exhibit greater dietary breadth (number and types of food items in the diet; (Tutin *et al.*, 1997)) and frugivory levels when compared to higher elevation populations (Yamagiwa *et al.*, 1994, 1996, 2005). Western gorillas seem to exploit a wider frugivorous niche, with greater overall dietary diversity and greater fruit diversity in the diet than all Eastern gorillas (Doran & McNeilage 1998; Doran *et al.*, 2002; Doran-Sheehy *et al.*, 2009; Nishihara, 1995; Rogers *et al.*, 1990, Watts 1996; Williamson *et al.*, 1990; Yamagiwa *et al.*, 1994). These differences may reflect the fact that Western gorillas inhabit lower elevations with reduced herb densities and higher fruit availability than do mountain gorillas (Doran-Sheehy *et al.*, 2004; Masi *et al.*, 2009). Mountain gorillas ranging from 1160 to about 3700 meters above sea level (masl) experience very different habitats than Western lowland gorillas (Doran *et al.*, 2002; Masi *et al.*, 2009), which range from about 200-500 masl (Goldsmith 2003; McFarland 2007), and these environmental differences are evident in dietary differences both between and within species, as even neighboring populations at different elevations may exhibit large variation in diet (Robbins *et al.*, 2006).

These findings concur with two general patterns in primate feeding ecology. First, diet specialization in primates typically increases as degree of folivory increases (Hladik 1981; Watts 1984). Plant species diversity in the diet increases with the proportion of fruit in the diet (Tutin *et al.*, 1991), and gorillas in particular may reduce dietary breadth when fruit is scarce (Tutin *et al.*, 1997). Thus, apes with greater access to fruit are expected to be less specialized and eat a greater variety of food species than those forced to rely on mainly terrestrial herbaceous vegetation (THV) for sustenance. Second, diet is often strongly correlated with elevation, due to variation in fruit and herb availabilities along elevation gradients (Basabose, 2002; Goldsmith 2003; Hanya *et al.*, 2003; Masi *et al.*, 2009; Nkurunungi *et al.*, 2004; Robbins & McNeilage, 2003; Robbins *et al.*, 2006; Rothman *et al.*, 2006). Dietary disparities are often greater between high- and low- altitude gorilla populations than between low-altitude gorillas and other sympatric ape species (Doran & McNeilage 1998; Yamagiwa *et al.*, 1996), though niche differentiation between species becomes clearer in times of fruit scarcity (Head *et al.*, 2011; Stanford & Nkurunungi, 2003; Tutin *et al.*, 1991, 1997; Yamgiwa & Basabose, 2006, 2009). Similarities between mountain and Western lowland gorilla diets exist, and both species are selective eaters that consume some parts of a plant and leave other parts untouched (Doran-Sheehy *et al.*, 2009; Plumptre, 1995; Remis 2003; Rogers *et al.*, 1990). Dietary differences among populations are thus likely related to differences in food, particularly fruit, availability, variation in ecological conditions, and elevation range (Chapman & Chapman, 1999; Chapman & Fedigan, 1999; Robbins *et al.*, 2006).

While associations between access to fruit, elevation, and diet composition generally aid in predicting broad similarities and differences in the diets of Western and Eastern gorillas, such patterns actually highlight uncertainty surrounding the dietary composition of one very poorly studied subspecies of conservation concern, the Cross River gorilla (*Gorilla gorilla diehli;* hereafter: CRG). The CRG is a subspecies of Western gorilla found only in the Guineo-Congolian forests of Cameroon and Nigeria, and is the most critically endangered and least studied great ape (De Vere *et al.*, 2011; Oates *et al.*, 2007; Sawyer, 2012; Sawyer & Sawyer, 2011). CRGs constitute the most northern and western of all gorilla populations, which may include only 300 individuals divided into 14 fragmented subpopulations (Bergl & Vigilant 2007; Bergl *et al.*, 2008; Bergl *et al.*, 2011; De Vere et al 2011; Sarmiento 2003; Fig. 1). Although the CRG is both geographically and phylogenetically most closely related to Western lowland gorillas, CRG populations are unusual compared to other Western gorillas in that they occupy relatively higher and more varied elevation ranges (between 200 and 1800 meters) with resulting irregular food availability (McFarland, 2007). Most CRG subpopulations exist in ridge forests above 400 masl, where access is more difficult for hunters (Caldecott & Ferriss 2005; McFarland

2007; Oates *et al.*, 2003). The effects of these habitat disparities on the diet of the CRG remain largely unknown. Difficult terrain, historical hunting, lack of infrastructure, and the trans-national distribution of the subspecies make CRG challenging to study and protect, and many subpopulations currently exist outside of protected areas. There has been only one previous study of the CRG diet (McFarland 2007; Rogers *et al.*, 2004), which indicated that a relatively large number of species (168) was included, and that levels of frugivory were lower than Western lowland sites but higher than Mountain gorilla sites (90% of fecal samples contained evidence of fruit feeding), more comparable to mid-elevation Eastern gorilla sites (McFarland, 2007; Yamagiwa *et al.*, 1994). These results suggest that while CRG may share more food species Western lowland than Eastern gorillas because of their neighboring distributions, we expect CRG may exhibit diet patterns more expected by elevation and fruit availability than by proximity and shared evolutionary history.

The necessary first step both for a better understanding of the evolution and variability in the feeding ecology of great apes, and to inform effective conservation decision-making for critically endangered gorillas, is to gather data on the dietary ecology and ranging patterns of gorillas living in different ecological circumstances (Robins *et al.*, 2006). Food availability is an important limiting factor to species' abundance and distribution, and availability of herbs in particular has been hypothesized to play an important role in the evolution of African ape social structure and gorilla dietary selection (Doran-Sheehy *et al.*, 2009; Marshall *et al.*, 2009; Plumptre, 1995; Wrangham 1979, 1986). Current studies however, suggest that hunting and other human activities, rather than food availability, are responsible for the current patchy CRG distribution (Bergl *et al.*, in press; Oates *et al.*, 2007; Sunderland-Groves 2009).While limited data exist for the Afi CRG subpopulation (McFarland 2007; Fig 1), the remaining subpopulations have, to date, been left largely unstudied, and only the most basic understanding of CRG diet and range selection currently exists. In this study, I aimed to (1) compile a list of plant species eaten by one CRG subpopulation; (2) distinguish quantitatively important food species that may be used in conservation and landscape connectivity planning for CRG; (3) measure preference in CRG herbaceous food choices; and (4) determine whether differences exist in preferred food availability in areas selected and avoided by the CRG. As even neighboring populations may exhibit large variation in diet (Robbins *et al.*, 2006), and food preference may reflect not only habitat characteristics but also traditions particular to a given region or group (Nishihara 1995; Yamagiwa & Basabose 2006), this study also set out to examine differences in diet and preferences between two CRG subpopulations. Findings will inform further ecological research as well as conservation planning.

Methods

Study Site

We conducted surveys in the Northern Mone/Mount Oko region, part of the Mone/Mbulu forest system of the Southwest Province of Cameroon. This forest system is located in the Manyu division of the Southwest Province of Cameroon and represents one of Africa's biodiversity hotspots (Asaha & Fru 2005; Forboseh *et al.*, 2007; Nku 2004; (Fig 1)). The approximately 1000 km^2 area has an estimated human population of about 6,300 individuals, living within 30 villages (Asaha & Fru 2005). Local households depend mainly on subsistence hunting and agriculture, and educational, transportation, and medical infrastructure is generally lacking (Asaha & Fru 2005). The Northern Mone/Mount Oko region includes the northern portion of the 560 km^2 Mone Forest Reserve, commissioned as a production forest by the national government, and the Southern portion of the Mbulu forest, called Mt. Oko (Fig 1). Although it is state-owned, Mone remains under the *de-facto* control of local communities, and the Mt. Oko region, though largely untouched because of its rugged terrain, has no protected status (Asaha & Fru 2005). The Mone Forest Reserve faces high rates of illegal logging, and is currently being considered as either a possible logging concession or a possible pilot site for carbon-financing (REDD+).

We calculated a minimum convex polygon of all known gorilla sighting or sign locations over the last 10 years in the Mone-Mt. Oko region to delineate the site for this study. Location data were collected by trained local field assistants of the Wildlife Conservation Society's Takamanda Mone Landscape Project, directed at the time by one of the authors (AN). This area is thought to contain one of 14 CRG subpopulations, and I carried out all research for this study within the calculated polygon.

Feeding trail sampling

Cross River gorillas in Cameroon avoid humans, making direct observation nearly impossible, and habituation to observers has been discouraged to avoid risks associated with hunting vulnerability and habitat fragmentation (Sunderland-Groves *et al.*, 2009). I therefore relied on indirect sampling methods to gain at least a broad, basic understanding of the diet of this relatively unknown species (Doran *et al.*, 2002, Rogers *et al.*, 2004, Sunderland-Groves *et al.*, 2009). Each night all weaned individuals of gorilla groups make nests nearby one another, forming a nightly nest site (Ganas *et al.*, 2008; Schaller, 1963; Williamson, 1988). During the day, gorillas move between these nest sites, leaving characteristic remains of their feeding and movement (Rogers *et al.*, 2004). Gorillas trample vegetation, defecate, and discard the least nutritious portions of their food plants, resulting in an easily identifiable "feeding trail" (Ganas *et al.*, 2008; Rogers *et al.*, 2004). Gorilla feeding signs surveyed in this study included chewed, broken, and discarded vegetation. Generally, indirect sampling methods should include both feeding trail and fecal sample analyses, as fecal samples provide a good assessment of diversity and frequency of fruit consumption, while feeding trails are important for detecting leaf and pith items in the diet (Doran-Sheehy *et al.*, 2006). I did not analyze fecal samples, and this study relied instead only on feeding trail analysis. Therefore, the strength of this study lies in the analysis of types, frequency, and preferences for herbaceous and shrubby species in the CRG diet, while it likely significantly underestimates food items from trees, particularly fruit (Doran-Sheehy *et al.*, 2006).

Between November 2009 and August 2010, I conducted guided and travel reconnaissance surveys with a team of assistants to search for gorilla feeding sign and nest sites within and adjacent to the study area. Guided reconnaissance surveys followed the path of least resistance while deviating no more than 40° from a set compass bearing (Kuhl *et al.*, 2008; McNeilage *et al.*, 2006) and consecutive surveys were placed <500 meters apart to avoid missing gorilla sign. Surveys were conducted at progressively farther distances from Nga village, until the entire study area was covered. When we found recent gorilla sign we abandoned the compass bearing, and followed the CRG feeding path (travel survey). We searched for recent gorilla feeding trails, and followed these trails for as long as possible. I aimed to follow feeding trails from one nest site to the next, to ensure that feeding trail analyses were complete. In reality, difficult terrain, lack of understory vegetation, and lack of unidirectional movement by the gorillas created significant challenges. Complete nest-to-nest follows were achieved on fewer than ten occasions, and distance traveled along feeding trails was not recorded because of frequent loss and re-discovery of trails, making cross-study comparison challenging.

Along feeding trails, I recorded all species and plant parts eaten. I also noted presence or absence of fruit seeds in any dung observed on the feeding trail and at the nest sites, as a rough indicator of minimum frugivory levels, rather than an exact measure of fruit consumption. Fruit species in the diet were identified strictly from trail sign; seeds in the dung were not used to identify fruit species consumed, leading to an underestimation of fruit species in the diet. Four or five team members consisting of a botanist, 2 local trackers, a local gorilla guardian, and the author collected data on 21 days per month over the ten month period, totaling 210 sampling days.

Surveys totaled 262 km, and included observation of 601 feeding signs from 508 feeding sites along 79 feeding trails (days) over the ten month period (Table 1). Feeding sign included chewed, broken, and discarded vegetation from a given plant species, and sign from more than one species within a 50 m distance was considered a single feeding site. Gorilla feeding sign and was differentiated from monkey, rodent, or ungulate feeding by experienced trackers using teeth marks, footprints, characteristics of the plant remains (i.e. pith removed versus tips removed), and other trail sign. I defined a feeding trail as all feeding remains and gorilla sign judged to be from a single day. In two months (May and June 2010), I observed less than five feeding signs, so I excluded these months from all analysis beyond the initial compilation of species in the CRG diet (Table 1). My analyses therefore encompassed eight months, spanning both wet and dry seasons. On average, we found 10 feeding trails per month (range: 2-16; Table 1).

Herbaceous Resource Availability

We carried out herbaceous resource assessments within 477 circular vegetation plots (10 m diameter), placed at 500 meter intervals along both guided and travel reconnaissance trails. I determined availability by counting the number of stems of each herbaceous species within each plot. Because we knew very little about the foods of this subpopulation at the start of the study, I included all species deemed potential CRG herbaceous foods from McFarland's Afi study (2007) and a Kagwene pilot study by SS. I counted 21 herbaceous species, 15 of which were identifiable to the species level. 253 of the 477 vegetation plots were located within the calculated CRG subpopulation range (see section subpopulation range analysis section for range calculation methods), and of those 169 were located in areas used by the CRG, while the remaining 84 were located in areas within the CRG range where we found no CRG sign. The large sample size along guided reconnaissance surveys rather than feeding trails within the CRG range should minimize bias that may arise from CRG selecting areas of high herb densities within their range. Study limitations prevented us from enumerating fruit species and precluded phenological studies. Measures of preference could be derived only for herbaceous species. Further research will be necessary to examine availability and seasonality of fruit food species in this region.

Subpopulation Range Analysis

To determine habitat areas utilized by CRG in the study region, I recorded all signs of gorilla presence along guided and travel reconnaissance surveys. Gorilla signs included nest sites, trampled vegetation, dung, and feeding sign (see above). I recorded 201 nest sites and 79 feeding trails total. Using these data, I calculated a CRG subpopulation range employing the Local Convex Hull (LoCoH) modeling technique (Calenge 2006; Ryan *et al.*, 2006; Sawyer, 2012). LoCoH applies Minimum Convex Polygon construction to a subset of localized data, resulting in a set of nonparametric kernels whose union represents a utilization distribution (Getz *et al.*, 2007). LoCoH may be the most robust, error-free home range analysis method (Getz *et al.*, 2007), and performed best in a model comparison for CRG (Sawyer, 2012). To minimize problems arising from spatial autocorrelation, I used all gorilla nest-sites and only one feeding sign per day, for a maximum of 2 location points for each day of gorilla use (De Solla *et al.*, 1999; Hayward *et al.*, 2009; Swihart & Slade, 1985). I randomly selected one data point from each feeding trail day, for a total of 279 data points in the analysis, resulting in an estimated range size of 31.73 km^2 (Sawyer in review). An area-accumulation curve indicated that estimated range area reached an asymptote with 150 location fixes, suggesting that I had enough data to estimate accurately the approximate subpopulation range (Sawyer, 2012). Range should ideally be calculated for individual groups, rather than subpopulations. However, I was unable to determine if one or multiple groups inhabited the study site, likely because of the flexible grouping patterns and frequent re-use of nest sites observed in CRG (McFarland, 2007; Sunderland-Groves *et al.*, 2009). I therefore used an overall subpopulation range for food selection analyses.

Diet Analysis

Important Foods: While food species importance may be defined by frequency in the diet, micronutrient supplementation, or biomass representation, I followed previous ecological studies by defining importance in the diet by relative representation of each food plant part in the observed diet (Rogers *et al.,* 2004). Important species were defined as fibrous (vegetative) species consumed on 5 or more (6%) of the observed feeding trail days, or fruits consumed on greater than 3 (~3.8%) or more days (Doran *et al.*, 2002; Ganas *et al.*, 2004). While other studies of gorillas have designated as important those vegetative species consumed on >5% of days and those fruits consumed on >1% of days (Doran *et al.*, 2002; Ganas *et al.*, 2004; Robbins *et al.*, 2006), I used a cut-off of 5 and 3 days because of the small number of days observed in this study (n = 79 days). The list of important fruit species is likely an underestimation, because of the study limitations discussed above, and represents only a first step in understanding frugivory of the CRG.

We further categorized important food species as staple, seasonal, or fallback foods. Western gorillas are selective feeders that prefer ripe fruit when available, incorporating a greater variety of leaves and herbs in the diet during months of fruit scarcity (Calvert 1985; Doran-Sheehy *et al.*, 2009; Goldsmith, 1999; Rogers *et al.*, 1990; Williamson *et al.*, 1990). Fallback foods, those consumed in inverse proportion to the availability of preferred foods (Marshall *et al.*, 2009), can therefore be considered those foods consumed mainly in months when fruit is scarce, while staple foods should show no difference in levels of consumption throughout the year. I did not directly measure fruit availability, and instead used data gathered for the Afi CRG subpopulation, indicating August-January as fruit-scarce months, and February-July as fruit-rich months (McFarland 2007). I defined important foods as staple, seasonal or fallback. Staple foods were eaten on a daily/weekly basis throughout the year (no significant difference between consumption in high and low fruit months). S*easonal* foods would ideally encompass those present in a majority of samples when available; however, as I did not conduct phenology studies and underestimated fruit consumption, I considered seasonally important species as those for which all observations occurred during only one season (fruit rich: February-July, or fruit poor: August – January), assuming that that this was when they were available. Phenological studies will be necessary to confirm whether this assumption was valid, and results should be interpreted cautiously. *Fallback* foods were always available (found within herbaceous resource plots throughout the study period) but eaten only or mainly during fruit-scarce months (greater than 70% of observations during fruit scarce months, following McFarland 2007) (Doran *et al.*, 2002; McFarland, 2007; Rogers *et al.*, 2004). I did not have sufficient data to separate fallback foods into 'staple' versus 'filler' categories and I recommend further research in the area to facilitate this distinction (Marshall *et al.*, 2009; Yamagiwa & Basabose, 2009).

Preference: Importance of a food species in the diet does not necessarily indicate preference. I therefore calculated preference for herbaceous species using Spearman rank correlations and Ivlev's Electivity Index (Ganas *et al.*, 2008). These methods compare the rank importance of each food in the diet to the rank availability of the food item in the gorilla range (e.g., "use vs. availability"; (Ganas *et al.*, 2008)). Species that are common in the diet, but also common in the habitat, will have low preference scores, as will species that are uncommon in the diet. Species that are common in the diet relative to their availability in the habitat will show high preference scores. I was able to calculate frequency and availability for only fifteen herbaceous species that I could identify to the species level within vegetation sampling plots and feeding remains. Additional food species, including those not identified to the species level, appeared too infrequently (or never) in the diet to include in the analysis. I calculated availability of individual food items using stem counts within the 262 circular vegetation plots that fell within the CRG subpopulation range. Frequency of each food item in the CRG diet was calculated as total number of sites at which remains of a species were encountered over the entire study period. A relative rank from one to fifteen was then assigned for both frequency in the CRG diet and availability within the determined subpopulation range for each of fifteen food species (Ganas *et al.*, 2008). A higher rank indicates greater availability or greater number of feeding sites at which the species was observed (Ganas *et al.*, 2008). For food species with the same availability or diet frequency, I assigned tied ranks. Ivlev's Index was calculated as: I = $(r_d - r_a)/(r_d + r_a)$, where $\mathbf{r_d}$ is the rank in the CRG diet and $\mathbf{r_a}$ is the rank in availability or abundance in the CRG subpopulation range (McNeilage 2001; Ganas *et al.*, 2008). Results indicate relative preference of food species compared to other herb species in the CRG diet, not an absolute measure of inclusion in the diet relative to all species in the habitat.

Food Availability and Range Selection: To test whether availability of herbaceous foods may play a role in CRG subpopulation distribution patterns, I compared herbaceous food species stem counts inside the identified subpopulation range to those outside of the range. Using Mann-Whitney Wilcoxon rank tests, I compared densities for the 15 food species I was able to count within vegetation sampling plots to determine if CRG may select areas based at least in part on availability of important herbaceous food species (Dobbs *et al.*, 2009; Sachro *et al.*, 2005; Sokal & Rohlf, 1995).

Research Ethics

This study complied with research regulations of the University of California, Berkeley, and the Cameroonian Ministry of Forestry and Wildlife (MINFOF). All work conformed to the laws of both Cameroon and the United States, and the ASP principles for the ethical treatment of nonhuman primates.

Results

Cross River gorillas in the Mone/Mt Oko area included in their diet 141 plant parts from 102 different plant species representing 40 families (Appendix 1). Botanist Okon Felix identified 85 of the observed species to at least the genus level, while 17 species were unidentifiable but distinguishable as unique. Half of the 508 observed feeding signs represented only 12 plant parts from 9 species (shown in bold in Appendix 1). CRG diet included 23 important species, 14 of which appeared in the CRG diet in half or more of the 8 sampled months (Table 2). Important plant types included two lianas, eleven herb species, and ten trees (Table 2). Important plant parts included leaves of both herbs and trees, pith of herb and palm species, bark of both trees and lianas, and six fruit species (Table 2). The species appearing most frequently in the diet were *Landolphia spp* (45 days), *Cercestis camerunensis* (24 days), *Palisota sp 1* (24 days), *Leea guineensis* (18 days), *Stylochaeton zenkeri* (18 days), and *Aframomum sp 1* (16 days; Table 2). I detected three seasonally important fruit species (Table 2). The low number of seasonally important species likely reflected the low detection rate for fruit feeding due to lack of fecal sample analyses, and the lack of data from May and June, two rainy season months when fruit is likely to play a major role in CRG diet (Cipolletta, 2004). I detected six fallback species, mainly herbaceous (Table 2). Leaves, in addition to herbs, are important gorilla fallback foods during times of fruit-scarcity, and our trail-sampling methodology likely missed important leaf species in the CRG diet (Doran-Sheehy *et al.*, 2006; Doran-Sheehy *et al.*, 2009).

Of the 23 important food species detected in the Mone CRG subpopulation, ten were also important in the Afi CRG subpopulation (Table 3; McFarland, 2007). Thirteen of the food species important to the Mone CRG subpopulation were not important in the Afi subpopulation, and 11 of those do not even appear in the Afi subpopulation diet (Table 3). Twenty-six of the 37 important food species in the Afi subpopulation were not important in Mone, and 15 of those did not appear in the Mone diet (Table 3).

Of the 15 herbaceous species measured, the Mone CRG subpopulation preferred 6 species, and showed no preference or partially avoided the remaining 9 (Table 4). One of the 15 measured species, *Dracaena arborea*, was never observed eaten by this subpopulation of CRG. The highest preference values were calculated for *Acanthus montanus* and *Anchomanis difformis*, which appeared very rarely in the diet, but even more rarely in the subpopulation range. Observed preferences for *Cercestis camerunensis, Palisota spp, and Aframomum spp*, which were highly available in the subpopulation range, but appeared more than expected in the diet, may therefore be more informative (Table 4). While *Stylochaeton zenkeri* was very common in the CRG diet, this apparently reflected its high availability rather than a preference for the species (Table 4).

Average herbaceous food availability across the study site appeared similar to other Western gorilla sites (0.57 stems/m^2; Table 5). However, direct comparisons can be made to one study only (Doran *et al.*, 2002) because I counted stems only of potential CRG food species, while many other studies included all herbaceous species (Table 5). I observed Thirteen herbaceous species in both vegetation sampling plots and in the CRG diet, 9 of which showed trends towards higher average stem densities within than outside the CRG subpopulation range ($p<0.1$), 6 of which were statistically significant ($p<0.05$; Table 6). Four of the five herbaceous species for which CRG exhibited positive preference had higher stem densities within than outside of the CRG range (Table 6).

Discussion

Diet and food availability influence both the ecology and the conservation of critically endangered species like the Cross River gorilla. Biomass may be largely determined by the availability of staple and fallback foods during ecological "crunch times" (Oates *et al.*, 1990; Tutin *et al.*, 1997) while persistence in fragmented habitats is strongly influenced by frugivory levels in non-crunch times (Boyle & Smith, 2010; Johns & Skorupa, 1987). Gorilla densities are highly dependent on preferred herb species densities (Brugiere & Sakom 2001; Rogers *et al.*, 2004), while gorilla ranging and activity patterns are influenced by seasonal frugivory (Cipolletta 2004; Masi *et al.*, 2009). Therefore, a better understanding of the Cross River gorilla (CRG) diet can increase ecological knowledge of the subspecies and assist in developing effective conservation management strategies. This study contributes to an understanding of the diet of the little known CRG by adding data from a second study site to initial findings (McFarland 2007). While limited in scope, our results confirm that CRG in the Mone/Mt. Oko region not only show preference for certain foods (Table 4), but may also prefer to range in areas with higher availability of preferred foods (Table 6). Our results also highlight some of the important food species in the CRG diet that will require further ecological study (Table 2) and may facilitate initial broad comparisons between CRG subpopulations (Table 3) and between gorilla subspecies (Table 5).

Gorilla diet is particular to specific regions due to both local traditions and local environmental conditions (Nishihara 1995), and previous studies indicated that CRG diet shows both similarities and differences relative to other Western gorilla populations. In a comparison across Western gorilla sites, the Afi CRG population had the highest proportion of unique important food species, those that were either not eaten or not important at any other site (McFarland, 2007; Rogers *et al.*, 2004). Additionally, Afi CRG showed frugivory levels more similar to mid-elevation Eastern gorilla populations than their Western gorilla neighbors (90% and 89% of fecal samples contained fruit in Afi and Itebero respectively, while almost 100% of Western lowland samples generally contain fruit; (McFarland, 2007); Table 5). However, Afi CRG live in areas with similar herb densities to many Western lowland sites, eat a large number of different species (168 species eaten; (McFarland, 2007); Table 5), and share many food species with other Western gorilla populations (Rogers *et al.*, 2004).

This study also reveals both similarities and differences between CRG and Western gorilla diets. The Mone CRG population, unlike other Western gorilla populations, relies heavily on Araceae species (Tables 4 & 6; (Rogers *et al.*, 2004)), perhaps because of differences in availability across sites. Additionally, in Mone, *Leea guineensis* fruit, unimportant in some Western lowland gorilla diets, and completely ignored by others, is one of the CRG's important staple species (McFarland, 2007; Tutin *et al.*, 1991; Williamson *et al.*, 1990). *Leea guineensis* fruit is so popular with Mone CRG that it is locally referred to as "the peanut of the gorillas", an allusion to a staple in the local human diet. Overall herb availability appears similar between CRG and Western lowland gorilla sites (McFarland 2007; Table 5) and I found that Zingiberaceae and Commelinaceae species, particularly *Aframomum and Palisota spp*, are similarly important staple species for the CRG as in other Western Lowland populations (Doran *et al.*, 2002; Nishihara, 1992; Rogers *et al.*, 2004). Additionally, Marantaceae species appear to play a fallback role in the CRG diet, and like the gorillas in Lope, the Mone CRG relied on *Marantochloa purpurea* in periods of low-fruit availability, despite its likely constant availability (Tutin *et al.*, 1997). Finally, *Landolphia spp* are staples for Mone CRG like many other Western gorillas (Rogers *et al.*, 2004).

Even within the CRG's small geographic range, diet may vary greatly. While genetic analysis shows recent movement between most of the CRG subpopulations (Bergl & Vigilant, 2007; Bergl *et al.*, 2008), I discovered some dietary differences between subpopulations in this study (Table 3). Overlap in important species with the Afi subpopulation was low, with fewer than half of important food species being shared, and more than half of important species not even appearing in the other subpopulations diet (Table 3). For example, *Dracaena arborea* is one of most important leaf species for gorilla in Afi (McFarland, 2007), and local hunters report that the Mbulu subpopulation eats *Dracaena arborea* pith on a regular basis (unpublished data). However, Mone gorillas were never seen to eat *D. arborea* during this study, and local staff members report that the Kagwene subpopulation does not eat the species either, despite its abundance in the habitat (unpublished data). Additionally, *Cercestis camerunensis* was one of the most important and preferred foods observed in the Mone CRG diet, but appears in neither the Afi, nor the Kagwene diet (McFarland, 2007; unpublished data). As has been shown for neighboring populations of other primates (Chapman & Chapman, 1999; Robbins *et al.*, 2006), important food species for neighboring CRG populations may be quite different due to local ecological conditions. Additional research will be necessary both to better understand the differences in food availability and diet between the Afi and Mone subpopulations, and to investigate the additional 12 subpopulations. Our preliminary findings suggest that, within the CRG's range, conservation strategies should include subpopulation specificity.

CRG live in fragmented subpopulations, and the selection by the CRG of areas with high availability of preferred foods indicates that maintaining connectivity will likely require protection of habitats that contain preferred food species. Given that herbs are a keystone resource for gorillas (Brugiere & Sakom, 2001) and can serve as an important buffer when fruit is scarce (Yamagiwa *et al.*, 1994), high availability of preferred herb species like *Cercestis camerunensis, Palisota spp,* and *Aframomum spp* may indicate areas of great conservation value for CRG. In the Mone/Mt. Oko area, slope and elevation appear to have negative correlations with abundance of *Palisota, Aframomum*, and *C. camerunensis* (Sawyer unpublished data), highlighting the potential importance of lower slope and elevation sites for the viability of CRG populations. Additionally, another important species in the diet, *Leea guineensis*, is thought to grow more readily in areas of human disturbance (Okon Felix pers comm). While research to date has directed CRG conservation strategies towards steep, high elevation sites (Bergl et al in press; Oates *et al.*, 2007), this study indicates that conservation actions should also target flatter, more disturbance-prone regions. Gorilla habitat management will likely be more successful with a better understanding of how important food species help maintain CRG subpopulations (McNeilage, 1995; Rothman *et al.*, 2006) and the tradeoffs CRG make between food availability and risk of human contact (Sawyer unpublished data).

Recommended Future Directions

Though this study represents foundational research on the little known Cross River gorilla, it is limited in several important ways. Firstly, comparison of fruit species consumed and frugivory levels between the Mone CRG and other gorilla populations were not addressed, and further research will be necessary to measure frugivory in the diet and habitat of the Mone CRG population. I likely significantly underestimated the number of fruit species in the Mone CRG diet because gorilla sign was not found during the rainy season months of May, June, and September, and dung samples were not collected and analyzed for seed content. While visual examination of fresh dung at 245 nest and trail sites revealed fruit seeds in 122 dung samples (about 50%), our study methods were not comparable to other studies (Table 5). Additionally, the diversity of foods taken from trees, and the presence of highly digestible foods, will be underestimated unless regular observation of gorillas is possible (Rogers *et al.*, 2004) and no observation of CRG was possible during this study. While such conditions may persist in the Mone area in the foreseeable future, other subpopulations, like Afi and Kagwene, where long-term research and law enforcement staff are continuously present, may provide more opportunities for direct observation. While this study cannot assess differences in dietary traditions among sites and subspecies, it rouses questions for future investigation into local traditions within and among CRG subpopulations.

Secondly, the clear effect of study length on dietary analyses of gorilla populations suggests that this study has underestimated the overall diversity of the CRG diet (Rogers *et al.*, 2004; Tutin & Fernandez, 1993). Logistical challenges constrained study length, and the team was unable to find any gorilla sign during multiple months of the study period, further weakening the conclusions and likely underestimating fruit relatively more than other species. I recommend longer studies, which would require additional funding, infrastructure, staff, and expertise.

Finally, research to analyze fecal contents and complete nest to nest follows will better elucidate frugivory and nutritional patterns within the CRG diet. The CRG is the least studied of all gorillas, and its fragmented subpopulations and critically endangered status demand that we put immediate efforts towards both a better understanding of the subspecies' ecology and implementing conservation efforts on the ground. I hope this research serves as both a foundation and a call for additional research in the Cross River gorilla region.

Figures and Tables

Figure 1.

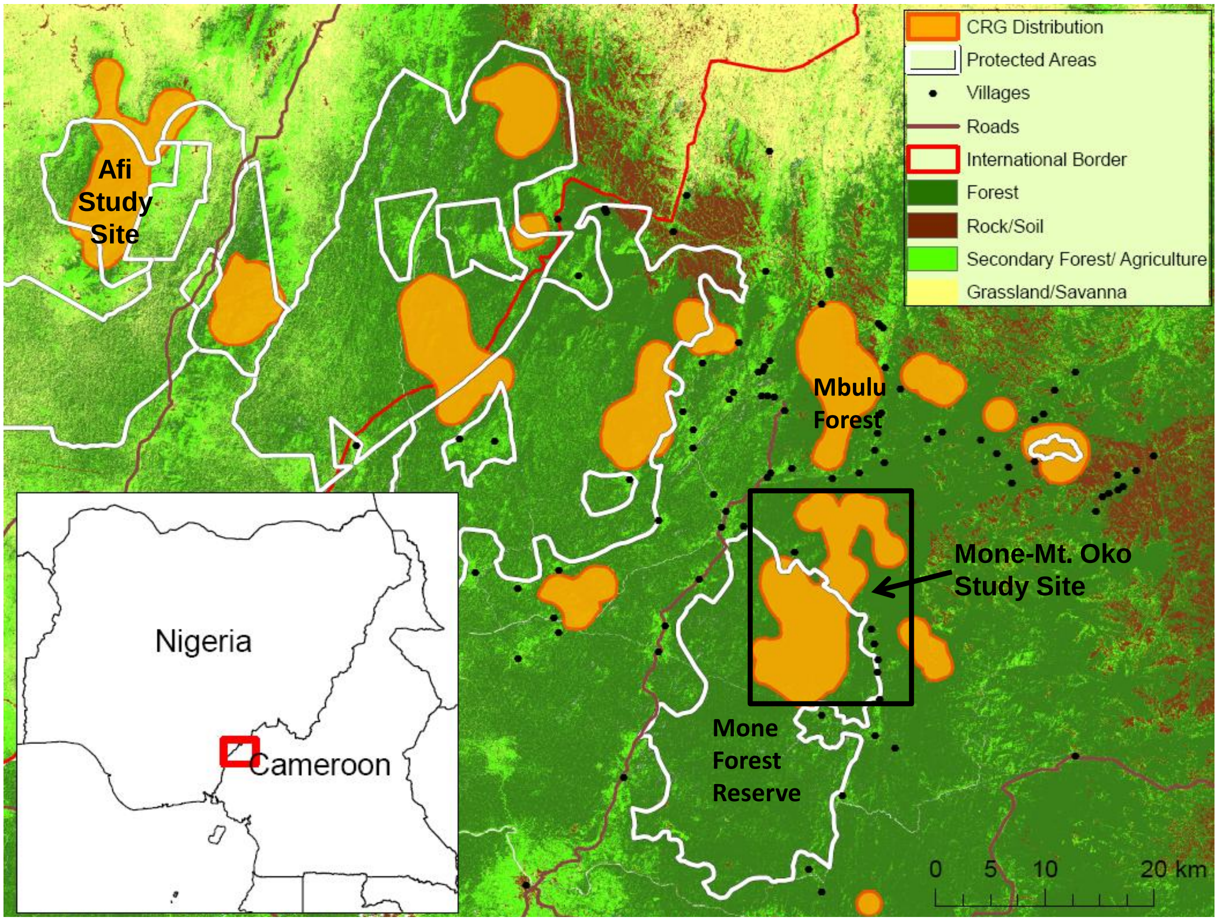

Table 1. Number of gorilla sign, feeding sites, and feeding trails observed per month over the study period.

Month	**Trails**	**Sites**	**Sign**
Nov 2009	14	175	200
Dec 2009	13	109	141
Jan 2010	13	27	30
Feb 2010	16	102	128
Mar 2010	2	5	6
Apr 2010	5	14	17
May 2010*	1	1	1
Jun 2010*	1	1	1
July 2010	8	55	58
Aug 2010	6	19	19
Total	**79**	**508**	**601**

* Because only one feeding sign was observed for the months of May and June, these months were excluded from further analysis, leaving four fruit-rich and four fruit-scarce months in the analysis

Table 2. Important species in Cross River gorilla diet, ordered by percentage of days observed in the diet*

Type**	**Species**	**Parts Eaten**	**Sites**	**Days**	**Months**	**% Sites**	**% Days**	**% Months**	**% Sites in Fruit Rich mos.**
Staple	*Landolphia sp*	leaves, bark, fruit	108	45	8	21%	57%	100%	50%
	Palisota sp 1	leaves, pith	48	24	6	9%	30%	75%	43%
	Cercestis camerunensis	pith	58	24	6	11%	30%	75%	38%
	Leea guineensis	leaves, fruit, pith	22	18	6	4%	23%	75%	54%
	Stylochaeton zenkeri	leaves	33	18	5	6%	23%	63%	36%
	Aframomum sp 1	pith	25	16	7	5%	20%	88%	60%
	Pycnanthus angolensis	leaves, pith, bark	19	13	3	4%	16%	38%	40%
	Musanga cecropioides	leaves, pith, bark	16	11	5	3%	14%	63%	36%
	Laccosperma opacum	pith	15	10	6	3%	13%	75%	69%
	Guarea thompsonii	leaves	15	9	4	3%	11%	50%	43%
	Trilepisium madagascariense	leaves, fruit	9	8	5	2%	10%	63%	47%
	Unknown liana 1	pith	9	7	3	2%	9%	38%	53%
	Nephthytis sp	leaves	5	5	4	1%	6%	50%	86%
	Aframomum sp 2	pith	5	5	5	1%	6%	63%	50%
	Myrianthus arboreus	bark	5	5	2	1%	6%	25%	50%
Seasonal	*Pseudospondias microcarpa*	fruit	6	5	4	1%	6%	50%	100%
	Cola cimicapaphila	fruit	3	3	1	1%	4%	13%	100%
	Staudtia kamerunensis	fruit	3	3	1	1%	4%	13%	0%
Fallback	*Urera rigida*	leaves	15	11	4	3%	14%	50%	25%
	Ficus sp	leaves, pith, bark	12	7	2	2%	9%	25%	0%
	Acanthaceae sp 1	leaves, pith	7	6	2	1%	8%	25%	5%
	Marantochloa purpurea	pith	7	5	3	1%	6%	38%	27%
	Costus afer	leaves, pith	5	5	3	1%	6%	38%	27%
	Eremospatha wendlandiana	pith	5	5	2	1%	6%	25%	0%

* Important species defined as fibrous (vegetative) species consumed on 5 or more (6%) of observed feeding trail days, or fruits consumed on greater than 3 (~3.8%) or more days (adapted from Doran *et al.*, 2002; Ganas *et al.*, 2004).

** Staple foods were eaten on a daily/weekly basis throughout the year (no significant difference between consumption in high and low fruit months). S*easonal* foods were those for which all observations occurred during only one season (fruit rich: February-July, or fruit poor: August – January). *Fallback* foods were always available (found within herbaceous resource plots throughout the study period) but eaten only or mainly during fruit-scarce months (greater than 70% of observations during fruit scarce months (Doran *et al.*, 2002; McFarland, 2007; Rogers *et al.*, 2004).

Table 3. Comparison of Food Species Important to the Mone and Afi[1] Cross River gorilla (CRG) Subpopulations**

Important in Both Mone & Afi CRG	**Important only in Mone**	**Important only in Afi & appear in Mone diet**	**Important in Afi & do not appear in Mone Diet**
Aframomum sp 1	*Acanthaceae sp 1**	*Palisota sp 2*	*Dracaena arborea*
Costus afer	*Aframomum sp 2*	*Thaumatococcus*	*Turreanthus africanus*
Ficus sp	*Cercestis camerunensis**	*Hypsoldelphys*	*Morus mesozygia*
Landolphia sp	*Cola cimicapaphila**	*Anchomanes difformis*	*Gongronema latifolium*
Marantochloa purpurea	*Eremospatha wendlandiana**	*Treculia africana*	*Albizia zygia*
Musanga cecropioides	*Guarea thompsonii **	*Parkia bicolor*	*Pterocarpus osum/mildgraedii*
Myrianthus arboreus	*Laccosperma opacum **	*Sorindeia spp*	*Grewia mollis*
Palisota sp 1	*Leea guineensis*	*Chrysophyllum sp*	*Tabernaemontana pachysiphon*
Pseudospondias microcarpa	*Nephthytis sp**	*Antiaris toxicaria africana*	*Garcinia kola*
Pycnanthus angolensis	*Staudtia kamerunensis **	*Cola millenii*	*Dialium guineense*
Trilepisium madagascariense	*Urera rigida**	*Milicia excelsa*	*Vitex*
	*Stylochaeton zenkeri**		*Maesopsis eminii*
			Monodora mristica
			Uvariodendron calophyllum
			Stylochaeton warneckei

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1. From: McFarland 2007

* Does not appear in Afi diet

** Availability of all species at both sites is unknown, and requires further study

Table 4. Relative Preferences for herbaceous food species in the Mone CRG diet based on Ivlev's Electivity Index

Species	**Avg stems per 100 m^2***	**Feeding Sites Observed****	**Availability Rank**	**Diet Rank**	**Ivlev's Electivity Index**
Acanthus montanus	0.00	3	1	6	0.71
Anchomanis difformis	0.01	6	2	10	0.67
Aframomum sp	2.09	25	9	12	0.14
Costus afer	0.38	5	6	7	0.08
Palisota sp	5.25	48	12	14	0.08
Cercestis camerunensis	10.93	58	14	15	0.03
Acanthaceae spp	2.88	7	11	11	0.00
Stylochaeton zenkeri	29.31	33	15	13	-0.07
Marantaceae spp	2.17	5	10	8	-0.11
Nephthytis sp	7.05	5	13	9	-0.18
Commelina sp	0.14	1	4	2	-0.33
Hypselodelphys sp	0.28	1	5	2	-0.43
Dracaena arborea	0.05	0	3	1	-0.50
Megaphrynium sp	1.00	1	7	2	-0.56
Thaumatococcus sp	1.60	1	8	2	-0.60

*Averaged over 253 vegetation plots within subpopulation range

** Total number of sites at which remains of the species were observed, out of a total of 508 sites

Table 5. Comparison of Dietary Breadth, Frugivory, and Herbaceous Food Availability for the Four Gorilla Subspecies, ordered habitat elevation.

Site	Elev	Gorilla Species	# Items in Diet	# Species Eaten	# Fruit Species Eaten	% days fruit in diet	Avg. Herb Density (stem/m^2)	Study Duration (mo.)
Bai Hokou[4]	low	WLG	230	129	89	99	0.82	39
Loango[5]	low	WLG	203	145	82	81.5	0.26	52
Lope[6]	low	WLG	182-220	134	95-10	96-98	1.87	72+
Mondika[7]	low	WLG	127	100	70	99.8-100	0.78**	36
Ndoki[8]	low	WLG	182	152	115	100	2.25	12
Mone	mid	CRG	141	102	11	50*	0.571**	10
Afi[1]	mid	CRG	216	168	100	90.2	1.16	32
Itebero[2]	mid	ELG	194	121	48	89	no data	11
Buhoma[3]	mid	MG	187-205	104-113	31-36	69.7-82.1	6.5	12
Kahuzi[9]	high	ELG	231	116-126	20-59	0-56 (monthly), 96.5	1.03***	12+
Ruhija[10]	high	MG	106-160	62-105	11-30	65.6	24.2	12
Virungas[11]	high	MG	65-75	35-44	0-3	<1	no data	12&17

Species: Cross River (CRG), Eastern lowland (ELG), Mountain (MG), Western lowland (WLG).
Elevation: low < 500 m; mid 500-2000 m; high > 2000 m
Studies: 1) McFarland 2007; 2) Yamagiwa *et al.*, 1994; 3)Ganas et al 2004; 4) Remis 2002; 5) Head *et al.*, 2011; 6) Williamson *et al.*, 1990, Tutin *et al.*, 1991 & 1997; 7) Doran *et al.*, 2002; 8) Nishihara 1992 & 1995; 9) Yamagiwa *et al.*, 1996, Yamagiwa & Basabose 2009; 10) Ganas et al 2004, Rothman *et al.*, 2006, Stanford & Nkurungi 2003, 11) Watts 1984, McNeilage 2001.
* Visual assessment of 245 encountered feces for presence/absence of fruit seeds, not comparable to other studies where seeds in fecal samples were washed and identified
** Only species in gorilla diet
*** 10 species in chimpanzee diet (no data available on gorilla food densities) (Basabose, 2002)

Table 6. Comparison of Herbaceous Food Availability Within and Outside of Mone CRG Subpopulation Range.

Species	**Avg stem density Inside Range**[1,2]		**Avg Stem Density Outside Range**		**Z**	**P**	**% Days Eaten**	**CRG Preference (Table 4)**
Cercestis camerunensis	10.93	± 15.79	6.44	± 13.07	-3.82	<0.0001	30%	+
Stylochaeton zenkeri	29.31	± 42.16	20.85	± 39.45	-4.15	<0.0001	23%	+
Hypselodelphys sp	0.28	± 1.34	0.23	± 2.10	-1.96	0.025	3%	-
Palisota spp	5.25	± 8.39	5.66	± 11.97	-1.94	0.026	30%	+
Megaphrynium sp	1.00	± 9.64	0.00	± 0.00	-1.94	0.027	1%	none
Commelina sp	0.14	± 0.87	0.01	± 0.10	-1.7	0.045	1%	-
Aframomum spp	2.09	± 16.55	0.74	± 3.68	-1.43	0.076	20%	+
Acanthaceae spp	2.88	± 13.86	1.62	± 7.34	-1.41	0.079	8%	-
Costus afer	0.38	± 2.81	0.19	± 1.59	-1.3	0.097	6%	+
Anchomanis difformis	0.01	± 0.11	0.00	± 0.00	-1.11	0.133	5%	+
Thaumatococcus sp	1.60	± 24.02	0.08	± 0.83	-0.75	0.225	1%	-
Nephthytis sp	7.05	± 11.64	8.55	± 17.52	0.28	0.609	6%	-
Marantaceae spp	2.17	± 8.00	2.82	± 10.22	0.47	0.682	5%	-

1. stems/100 m^2
2. stem counts averaged from 156 vegetation plots outside and 253 vegetation plots within the CRG subpopulation range

CHAPTER 3

Subpopulation Range Estimation for Conservation Planning: A case study of the Mone Cross River gorilla Subpopulation

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Abstract:

Measuring and characterizing the area utilized by a population or species is essential for assessment of conservation status and for effective allocation of habitat to ensure population persistence. Yet population-level range delineation is complicated by the variety of available techniques coupled with a lack of empirical methods to compare the relative value of these techniques. This study assesses the effect of model choice on resulting subpopulation range estimation for the critically endangered and patchily distributed Cross River gorilla, and evaluates the conservation conclusions that can be drawn from each model. Models considered range from basic traditional approaches (e.g. MCP) to newer home range techniques such as Local Convex Hull (LoCoH). Overlap analysis comparing sub-sampled to complete data sets are used to evaluate the robustness of various modeling techniques to data limitations. Likelihood Cross Validation Criterion is employed to compare core range model performance. Results suggest that differing LoCoH models produce similar range estimates, are robust to data requirements, provide a good fit for core habitat estimation, and are best able to detect unused habitat within the subpopulation range. LoCoH methods may thus be useful for studies into habitat selection and factors limiting endangered species distributions. However, LoCoH models tend to overfit data, and Kernel methods may provide similar information about animal space use while supporting protection of larger swaths of critical habitat. Subpopulation range analyses for conservation/management planning should therefore explore multiple modeling techniques, and employ both qualitative and quantitative assessments to select the best models to inform decision making for species of conservation concern.

Key Words: Conservation Planning; Cross River gorilla; Cross Validation Criterion; Home Range Analysis; Local Convex Hull

Introduction:

Measuring the extent and environmental attributes of area occupied by a population or species is essential for assessment of species conservation status (Burgman & Fox 2003, IUCN 2001), and for effective allocation of habitat to ensure population persistence (Schoener 1968; Kenward *et al.* 2001, Hodgson *et al.* 2009). Yet defining the area utilized by a population of conservation interest is not a straightforward task. Population-level habitat delineation is complicated by an almost overwhelming variety of techniques coupled with a lack of empirical methods to compare the relative value of these techniques and to allow consensus building (Lawson & Rogers 1997; Laver & Kelly 2008). Various forms of home range analysis can be used to delineate critical habitat at the population scale (Kenward *et al.* 2001), and each may lead to different conservation decisions. In this study, I utilize habitat-use observations for the critically endangered Cross River gorilla to explore effects of methodology on subpopulation range estimation and critical habitat prioritization for species conservation.

The Cross River gorilla (*Gorilla gorilla diehli;* hereafter: CRG) is one of the world's most endangered and least studied primates. CRG exist only in a patchy distribution in the southern portion of the Cameroon-Nigeria border region (Bergl & Vigilant 2007; Bergl *et al.* in press; De Vere *et al.* 2011) and may have as few as 300 individuals remaining, divided into 14 fragmented subpopulations (Bergl *et al.* 2008; Bergl *et al.* in press; De Vere *et al.* 2011; Sarmiento 2003). CRG have proved challenging to study and protect, and many of the remaining populations currently exist outside of protected areas. Very little is known about where the various subpopulations range on the landscape or why they occur in a patchy distribution within seemingly intact habitat. Active efforts are currently underway to identify critical habitat for landscape conservation efforts to protect the CRG in this biodiversity hotspot but, to date, a lack of understanding of the relationship between CRG ecology and available habitat has hampered conservation endeavors (Bergl *et al.* in press). In particular, very little is known about the ranging patterns of CRG subpopulations living in the Mone-Mbulu region and, despite the Cameroonian Government's 2002 Plan de Zonage recommendation that the Mone Forest Reserve be upgraded to a Wildlife Sanctuary, a lack of funding options has recently sparked discussions to open the Reserve as a logging concession (Forboseh *et al.* 2007). Studies estimate that forested areas available to individual CRG subpopulations range from only 4 to 35 km^2 and habitat conversion continues to decrease these numbers (Oates *et al.* 2003). Therefore, exploring the subpopulation ranging patterns of the CRG is both a critical first step in conservation planning for the subspecies, and can also help inform range modeling for other such patchily distributed species.

A subpopulation range is the geographic area representing the combined home ranges of all individuals or groups in the subpopulation. These home ranges are the areas traversed by an animal, or group, in pursuit of normal activities such as foraging, mating, or rearing young (Burt 1943; Lira *et al.* 2009; Seaman & Powell 1996). Range size and configuration are related to requirements and constraints dictated by species life history and physiological constraints, resource availability, climate and seasonality, geographic gradients, anthropogenic influence, and competition (Biebouw 2009; Hayward *et al.* 2009; Robbins & McNeilage 2003). Multiple methods are available to measure home ranges, ranging from simple polygons connecting the outermost data points (e.g. minimum convex polygon), to complex utilization density distributions. Though choice of method is known to influence results (Boyle *et al.* 2009; Grueter *et al.* 2009), there remains broad disagreement about when and where a given method should be applied (Laver & Kelly 2008). Inconsistency in methodology and reporting, especially across disciplines, makes comparison between home range studies challenging, and limits applicability to conservation decision making (Boulanger & White 1990; Kenward *et al.* 2001; Laver & Kelly 2008; Lawson & Rogers 1997).

While range patterns have been estimated for many Western gorilla (*Gorilla gorilla gorilla*) groups, CRG populations are unusual compared to other Western gorillas in that they occupy relatively higher elevations (between 200 and 1800 masl) with more varied topography and food availability (McFarland 2007; Chapter 2). Additionally, hunting by humans may influence CRG ranging patterns more strongly than other gorilla populations (Bergl *et al.* in press; Oates *et al.* 2007). Most CRG subpopulations are thought to exist in ridge forests above 400 masl, where access is more difficult for hunters (Caldecott & Ferriss 2005; McFarland 2007; Oates *et al.* 2003), but the impacts of the varied environment and human activities on the subspecies' ranging patterns have yet to be explored. Range size and location have only been delineated for the two highest elevation and most peripheral of the 14 subpopulations (McFarland 2007; unpublished data), and habitat prioritization to maintain connectivity between the subpopulations demands a better understanding of where the other subpopulations occur on the landscape and why. Here, I produce range estimates for a subpopulation of CRG using five of the most common home range methods: Minimum Convex Polygon, Grid Squares, Kernel Density Estimation, Cluster Analysis, and Local Convex Hull. I then compare model performance, draw conclusions about ranging patterns of Cross River gorillas in the Mone-Mt. Oko region of Cameroon, and examine the differing conservation conclusions that can be drawn from various models. From these conclusions, I recommend future directions for effective range analysis for management and conservation of the CRG and other patchily distributed species.

Methods

Study Site, and Data Collection

I conducted surveys in the Northern Mone/Mount Oko region, part of the Mone-Mbulu forest system, to assess one Cross River gorilla (CRG) subpopulation range. This forest system is located in the Southwest Province of Cameroon and represents one of Africa's biodiversity hotspots (Asaha & Fru 2005; Forboseh *et al.* 2007; Nku 2004). The Northern Mone/Mount Oko region is known to contain one of the fourteen subpopulations of CRG, and includes the northern portion of the Mone Forest Reserve and the Southern portion of the Mbulu forest, called Mt. Oko. The Mone Forest Reserve covers about 560 km^2, and is currently being considered as a possible pilot site in Cameroon for carbon-financing as an alternative to being managed for logging concessions. The Mt. Oko region, though largely untouched due to its rugged terrain, lies in an area surrounded on all sides by forest-dependent, developing villages. Few faunal studies of have been carried out in the area.

From November 2009 through August 2010, with a team of local assistants, I conducted guided reconnaissance surveys and guided travel surveys (McNeilage *et al.* 2006; Kuhl *et al.* 2008) in the region, searching for recent gorilla feeding signs and followed feeding trails to nightly nest sites. Guided reconnaissance surveys are similar to line transects, but follow the path of least resistance while deviating no more than 40° from a set compass bearing (Kuhl *et al.,* 2008), and were placed no more than 500 m apart to avoid missing CRG use of a particular area (McNeilage *et al.*, 2006). When we found recent gorilla sign we abandoned the compass bearing, and followed the CRG feeding path (i.e. guided travel survey). A total of 262 km of surveys were walked in this manner. Using a Garmin GPS and Cybertracker, location coordinates for all CRG feeding signs, trail signs, dung, and nest sites were recorded.

Subpopulation Range Calculation

Cross River gorillas in Cameroon avoid humans, making direct observation nearly impossible, and the potential for habituation has been rejected due to risks associated with hunting vulnerability and habitat fragmentation (Sunderland-Groves *et al.* 2009). Therefore, this study relied on indirect sampling methods to gain insight into the ranging patterns of this relatively unknown subspecies (Doran *et al.* 2002; Rogers *et al.* 2004; Sunderland-Groves *et al.* 2009). Gorillas live in social groups and all weaned group members construct nests in close proximity to one another each night, forming 'nest sites' (Ganas *et al.* 2008; Schaller 1963; Williamson 1988). During the day, groups move and feed between nest sites, leaving obvious trails of discarded food, feces, and trampled vegetation (Ganas *et al.* 2008; Rogers *et al.* 2004). These signs often remain visible for many months, can be accurately aged to reflect approximate date of gorilla habitat use, and can then be used to calculate ranges for gorilla groups and populations over one or multiple years (McFarland 2007). Home range should ideally be calculated for individual groups, rather than subpopulations. However, using cluster analysis, nest counts, and approximate nest dates, I was unable to determine if the study site consisted of one or multiple groups, likely due to the flexible grouping patterns, high home range overlap, and frequent re-use of nest sites observed in CRG (McFarland 2007; Sunderland-Groves *et al.* 2009). Therefore, for this study, I included all CRG signs found in the region to calculate the subpopulation range, rather than individual group home ranges. I used all CRG nest site fixes and one CRG feeding, trail, or dung location per day to minimize problems arising from spatial autocorrelation without removing the biological signals of interest (De Solla *et al.* 1999; Fieberg 2007; Hayward *et al.* 2009; Swihart & Slade 1985). I plotted an accumulation curve of the number of fixes versus estimated range area using the Minimum Convex Polygon method to ensure that an asymptote was reached and to measure the number of months of data required to estimate CRG subpopulation range (Harris *et al.* 1990, Laver & Kelly 2008; Hayward *et al.* 2009).

I calculated range estimates using five home range modeling techniques: Minimum Convex Polygon, Cluster Analysis, Grid Squares, Kernel Density Estimation, and Local Convex Hull. Minimum Convex Polygon (MCP) is the simplest and most popular home range analysis method (Getz & Wilmers 2004; Harris *et al.* 1990; Laver & Kelly 2008; Nilsen *et al.* 2008) and is therefore recommended by the IUCN in conservation planning (IUCN 2001). MCP analysis measures the smallest polygon in which no internal angle exceeds 180 degrees and which contains all sites or location fixes (Burgman & Fox 2003). Cluster analysis groups data using links that minimize mean joining distance (Kenward *et al.* 2001). After more than one cluster has formed, clusters merge when the outlier being added to one cluster is already a member of another and the process ends when all locations are assigned to the same cluster (the 100% MCP). Grid square analysis imposes a grid system of a chosen cell size on a map of location fixes and calculates the home range as the sum of each quadrant entered by the individual or group (Bermejo 2004; Cipolleta 2004).

Kernel Density Estimation (KDE) uses kernel smoothing from each data point to calculate range as a utilization distribution, or a probability density function giving the relative probability of finding an animal at any given location (Van Winkle 1975). The probability density function value at any point is the summation of the contributions of all kernels that overlap that point (Boyle *et al.* 2009; Horne & Garton 2006b) and a smoothing parameter, or bandwidth 'h', controls the width of the kernel (Worton 1989). Local Convex Hull (LoCoH) includes three types of algorithms, all of which construct a small convex hull (like MCP) around each point, and then incrementally merge the hulls together to form density isopleths (Calenge 2006; Getz *et al.* 2007). Isopleths depict the cumulative density of location fixes within a contour level (e.g. 5%, 10%,...100%), and can be used to find the probability density at any location by dividing its contour level minus the next smaller contour level by the area of the contour minus the area of the next smaller contour. Fixed K LoCoH applies the convex hull construction to K-1 nearest neighbors of each root point. Fixed r LoCoH constructs convex hulls out of all points within a designated search radius, 'r', of the root point. Adaptive LoCoH applies MCP to the maximum number of nearest neighbors such that the sum of their distances is less than or equal to a defined distance 'a' (Calenge 2006; Getz *et al.* 2007).

Minimum Convex Polygon (MCP), Cluster, Kernel Density Estimation (KDE), and Local Convex Hull (LoCoH) range analyses were conducted using the adehabitat statistical package in R and ArcGIS (Calenge 2006; R Development Core Team 2010). Grid Square range calculation was conducted in ArcGIS. All results were imported as raster or shapefiles into ArcGIS to facilitate mapping and area calculations. Grid Square analysis was calculated for both 500 x 500 meter and 250 x 250 meter grid cell size. This was done by overlaying a grid on the data points in ArcGIS, calculating the total number of grid cells entered by the CRG, and summing the area of all entered squares.

KDE models were calculated using ad hoc (Calenge 2006), maximum nearest neighbor distance (Getz *et al.* 2007), least squares cross validation (LSCV; Worton 1989), and likelihood cross validation (LCV; Horne & Garton 2006b) methods to determine h (bandwidth/search radius). Cell size was calculated as the first quartile of nearest neighbor distances. Isopleth levels were calculated at 5% intervals, and the 95% isopleths was used to calculate overall subpopulation range size (Harris *et al.* 1990). Three LoCoH methods were examined. The fixed K method was conducted for all 'K' values between 9 and 36 (Ryan *et al.* 2006). The Fixed r analysis was calculated for 'r' values between 0.4 and 2.0. The maximum distance between any two points in the dataset was used as the value of 'a' in the adaptive LoCoH (Getz *et al.* 2007).

Model Comparison

Sub-sampling overlap analysis was used to quantitatively compare model performances with respect to sample size (Trovati *et al.* 2010; Wilson *et al.* 2010). A random sub-sample of 150 location fixes was taken using R statistical package. All home range methods were then used to calculate the subpopulation range for the 150 points data set. Two comparisons were made between the subsample and complete data set to evaluate model performance, both assuming that the full set represents the "true" subpopulation range. First, the percentage of the total CRG location fixes included in the sub-sampled range was calculated. Second, the percentage overlap between the complete and sub-sampled ranges was calculated. Higher overlap and inclusion of location fixes indicated more robust models.

Additionally, following on Horne & Garton (2006a, b), I used likelihood cross-validation to compare home range model performance for the 50% core range (Stone 1974; Geisser 1975; Johnson & Omland 2004). Likelihood Cross Validation, is an information-theoretic model selection method comparable to Akaike's information criterion (AIC; Akaike 1973), but not restricted by the same assumptions and parameterization constraints (Horne & Garton 2006a; Stone 1974). Likelihood Cross Validation produces a Cross Validation Criterion (CVC) value measuring the relative goodness of fit, corrected for overfitting, of a home range model for a given set of animal locations.

The likelihood cross validation criterion is defined as:

$$\mathrm{CVC} = -2 * \sum \ln f_{-i}(x_i)$$

For i = 1 to n samples, where $f_{-i}(x_i)$ is the probability density calculated for sample x_i without the sample being used to calculate f. An iterative loop was employed to sum the log-likelihoods at each location without that location being used to estimate the model (Horne & Garton 2006a). Because CVC uses a log likelihood function, and would return an infinite value in the case where a location fix (x_i) fell outside of the re-calculated home range (f_{-i}), this comparative technique could only be used to evaluate model fit for the core 50% of the subpopulation range. Although evaluating performance for the 50% core range may lead to overfit models performing better than they would for the entire range, the core range can give important details about species habitat preferences and use patterns. CVC values were therefore calculated for 50% range regions for all methods to facilitate comparison. ΔCVC was calculated by comparing each CVC value to the smallest CVC value and was then used to determine relative support for each model and to choose the best model.

Results

Cross River Gorilla sign

Reconnaissance surveys resulted in 201 gorilla nest site location fixes, and 601 gorilla feeding/trail sign fixes from 78 days. Fresh sign was rare, and the challenging terrain, remoteness, and large study area size limited data acquisition. One data point was randomly selected from each day of feeding/trail sign, for a total of 279 data points in the analysis. Age of gorilla sign could be estimated by local trackers to within +/- one month using their knowledge of plant decomposition rates in the region. Though habitat use surveys were conducted over a 10 month period, because many forms of sign are detectable for at least 10-12 months, the sign recorded during these surveys represented gorilla habitat use over a total of 20 months (Table 1). I recorded more than 10 CRG location fixes from 9 of the 20 months, spanning both the wet (May – Oct) and dry (Dec – Apr) seasons. The area accumulation curve using the MCP method indicated that estimated subpopulation range area reached an asymptote with around 90 location fixes (Figure 1), indicating that enough data were collected to proceed with comparative subpopulation range analyses. A second asymptote was reached with approximately 150 location fixes, so I used 150 in model comparisons to be conservative. I was unable to determine how many individual gorillas were present in the region. Nest sites ranged from 1 nest to 18 nests in size, indicating the likelihood of more than one group in the area, flexible grouping patterns, and nest-site reuse. The most commonly encountered nest counts were 1 and 4, although 2, 3, 6, 8, and 9 were also quite common, emphasizing the difficulty I had in differentiating particular groups. Additionally, I observed no spatial patterns to the varying nest counts. Therefore, it is most likely that between 14 and 20 weaned individuals exist in this subpopulation, similar to preliminary estimates of 25 total individuals (Oates *et al.* 2003).

Subpopulation Range Analysis

The five common methods of home range analysis produced markedly different results when applied to data from surveys of the Mone/Mt Oko subpopulation of Cross River gorillas (Figure 2). Estimated 95% home ranges varied from 7.88 to 54.24 km^2 in size (Table 2, Figure 2). The MCP and cluster analyses resulted in the second largest area indicated by the five models employed (Figure 3). The grid square method for 500 x 500 meter cell size indicated a 95% range size of 16.75 km^2, while the same measure using 250 x 250 meter grid squares was less than half that size, the smallest of the resulting area calculations (Table 2, Figure 4a, 4b). The kernel density estimation (KDE) returned both the largest (h = half maximum nearest neighbor distance) and second smallest (h = LSCV) home range areas, depending on chosen bandwidth, and the LSCV kernel density estimation (h = 0.07449 km) resulted in an area of 38 discrete polygons, totaling only 9.48 km^2 (Figure 5). The KDE model using likelihood cross validation (LCV) to select bandwidth resulted in subpopulation range area estimates most similar to LoCoH models across isopleths (Table 2, Figure 2).

The fixed K Local Convex Hull (LoCoH) home range area was plotted for K values ranging from 9 to 36 and reached a local plateau at K values of both 18 and 33 (Figure 6a, 7a). Therefore, these two values were compared to the other models. The fixed r LoCoH home range areas were compared for search radius (r) values between 0.4 and 2 km, the likely range of CRG day journey length (Goldsmith 1999). The fixed r home range area did not plateau, but showed slight leveling of area at r values of 0.8 and 1.4, so these values were compared to other models (Figure 6b, 7b). The data set was too small to compute the 50% isopleths for search radii larger than 1.2 km, highlighting a major limitation of using this method for such a small data set. The 54% isopleth was therefore used in the CVC comparisons for r = 1.4. Adaptive LoCoH using a value of the maximum distance between two points (11.4 km) resulted in an intermediate home range size (Table 2, Figure 7c). Another plateau of the adaptive LoCoH was seen at an 'a' value of 15 (Figure 6c), so models using 11.4 and 15 were compared to the other models.

Model Comparison

The LoCoH models produced similar resulting subpopulation ranges at all range levels, while the MCP resulted in consistently larger areas than LoCoH and the Kernel methods varied widely in their results (Figure 2). Interestingly, the kernel model using likelihood cross validation to estimate bandwidth (h) produced area estimates very similar to those of the LoCoH models across home range levels (Figure 2). The Cluster and MCP home range methods had the greatest percentage of area overlap between the full and sub-sampled models (Table 3). The K LoCoH and Kernel density home range methods, on the other hand, contained the highest percentage of location fixes within the sub-sampled model (Table 2). On average, the K LoCoH model performed better than the other models, containing both a high percentage of total locations fixes (98.21%), and resulting in a high area overlap between the "true" and reduced models (96.34%).

The comparison of Cross Validation Criteria (CVC) values revealed striking differences among the five methods I used to estimate the Cross River gorilla subpopulation range (Table 2). The fixed r LoCoH method using a radius of 1.4 kilometers appeared to provide the best fit, having the most support from the data (Table 2). However, because the 54% isopleth was used in this case, it may not be directly comparable to the other methods. Adaptive LoCoH methods provided the next best fit to the data, using a distance of 15 kilometers, and both K LoCoH models provided good fits as well. The smaller grid-square analysis also provided a good fit to the core range estimate, not surprising given that grid-square methods are thought to be especially useful for delineating habitat cores. Kernel density and 0.8 km fixed r LoCoH methods (both involving a designated search radius) performed the worst. The LSCV Kernel performed better than the other Kernel procedures as it provided a comparatively tight fit around the core use areas (Table 2).

Discussion

Characterizing ranging patterns at a population level is essential for effective conservation decision-making for fragmented and threatened species, but a lack of consensus and empirical comparability of home range techniques decreases the value of such exercises for conservation and management. Similar to other studies, our findings indicate a major impact of study design on results, including critical habitat areas ranging from less than 10 to over 50 km^2 in size and including or excluding areas never visited by the study species. Likelihood cross validation criterion (CVC) assessment highlighted the value of newer home range techniques like Local Convex Hull (LoCoH) but also simpler methods like grid squares in identifying core habitat for endangered species, which may then be used to examine habitat selection and suitability. Choice of home range method will ultimately depend partly on study purpose, study scale, and amount of data the researcher is able to collect. For patchily distributed species like the Cross River gorilla (CRG), where limited data exist but immediate conservation action is necessary, the strengths and weaknesses of each home range modeling technique should be carefully considered.

When attempting to conserve as much area as possible for an endangered species, both Kernel density estimator (KDE) and Minimum Convex Polygon (MCP) may be beneficial, as they are often seen to overestimate home range size, a bias that may increase with sample size (Boulanger & White 1990; Boyle *et al.* 2009; Burgman & Fox 2003; Ryan *et al.* 2006; Seaman *et al.* 1999; Worton 1995). KDE and MCP returned the largest CRG subpopulation ranges in this study. However, KDE has advantages over MCP in that it includes a "buffer" area around the animal's critical habitat, and allows a more detailed understanding of animal space use within the home range (Grueter *et al.* 2009). MCP is still the most frequently used estimator because of its simplicity, and the notion that it is easily comparable across studies (Sekercioglu *et al.* 2007). However, Laver and Kelly's review (2008) challenged the idea that MCP is truly comparable between studies, noting sensitivity to the number of location fixes, sampling duration and design, and varied treatment of outliers as pitfalls facing the method's standardization. Therefore, if study goals include providing evidence for the protection of the maximum possible area, Kernel estimates are recommended over MCP (Borger *et al.* 2006). Nonetheless, as evidenced in this study, KDE is strongly influenced by bandwidth estimate. While LSCV is the most often recommended and most frequently used method for bandwidth estimation (Laver & Kelly 2008; Seaman and Powell 1996), some have noted that it can also cause major problems (Hemson *et al.* 2005; Horne & Garton 2006b). As bandwidth selection may have the greatest influence on KDE results (Silverman 1982; Laver & Kelly 2008), studies are needed to determine characteristics of animal space use and landscape ecology that may influence efficacy of selection methods. KDE should therefore be employed with caution in conservation decision making.

On the other hand, KDE and MCP may prove ineffective conservation tools in areas of high human pressure or human-conservation conflict. This study suggests that for species like the Cross River gorilla, living in subpopulations heavily influenced by human utilization, KDE and MCP will include high type II error rates and lack specificity necessary to assess habitat suitability and selection at a local scale (Pimley *et al.* 2005; Ryan *et al.* 2006). MCP is known to show very poor fit when home ranges are strongly non-convex (Burgman & Fox 2003; Getz & Wilmers 2004) and both the MCP and KDE for Mone/Mt. Oko CRG provided relatively poor fits for this population's long, narrow, concave distribution. These modeling techniques incorporated areas in the western and southern portions of the study site never visited by the CRG, which correspond to major footpaths connecting a hunting and fishing camp to multiple villages (unpublished data). Additionally, at a large scale, the CRG inhabit a highly fragmented landscape (Oates *et al.* 2003) and use of KDE methods over the species range may exclude potentially important areas between centers of activity (Type I error; Riley *et al.* 2003; Sekercioglu *et al.* 2007). Therefore, to minimize human-conservation conflict where conservation decisions may question traditional human land-use in critical habitat for endangered species, other modeling techniques may prove more effective conservation tools.

LoCoH home range techniques are thought to be the best methods for identifying and excluding unused areas within a home range (Getz & Wilmers 2004; Ryan *et al.* 2006) and the LoCoH methods performed better than other methods in this study. Adaptive LoCoH and fixed K methods resulted in the lowest CVC value, a high percentage of area overlap between the "true" and sub-sampled model, and a high rate of inclusion of total location fixes. This may be because LoCoH methods were successful in detecting a large region of unused habitat in the southwest portion of the CRG subpopulation range. This area coincides with the convergence of two large rivers, as well as the main footpath connecting Mbu village (along a motorable road) to the interior villages of Manta and Amebeshu. Foot traffic on the road is fairly regular, with numerous hunting sheds located along its borders (unpublished data). The 95% isopleths clearly show two polygons on either side of the major footpath, perhaps indicating a general avoidance by CRG of the area. LoCoH results may therefore best help conservation planners determine the limiting factors influencing ranging patterns of species like the CRG. Thus, both for attempts to determine geographic or anthropogenic barriers to species habitat use or movement, and for analyses of populations at fragmented scales, Local Convex Hull (LoCoH) may prove the best method. However, LoCoH is known to over-fit data, and therefore the 100% isopleth is likely to be an underestimate of the true space required by the subpopulation. Conservation planners must take this underestimate into account when delineating critical habitat.

Grid square methods are useful in exploration of habitat use, but not in determining overall home range size (Harris *et al* 1990). Despite warnings to the contrary, primate studies still rely heavily on this method, making comparisons between this and other gorilla studies quite difficult (Harris *et al.* 1990; Robbins & McNeilage 2003). As indicated by the low CVC value for the core range, grid square methods may be particularly useful for determining core habitats (Doran-Sheehy *et al* 2004), which can then be used in resource selection and habitat suitability analysis. However, the grid square method was heavily influenced by the chosen cell size, resulting in one estimated overall range size that was more than double the other (Table 2). Additionally, grid square analysis will significantly underestimate range size if animals are not intensively followed, and is therefore inappropriate for range estimation for difficult-to-study populations such as this one (Pimley *et al* 2005; Robbins & McNeilage 2003). Thus, this method should be combined with one of the other methods if overall study goals include range size determination.

The Cross River gorilla (CRG) represents an ideal species for which to explore subpopulation range modeling, as a better understanding of CRG spatial ecology is required to inform immediate conservation action. To date, a lack of knowledge of CRG habitat use plagues decision-making (Bergl *et al.* in press), and this study represents an important step towards a clearer understanding of CRG habitat use. However, delineating range patterns is just the first step in identifying the ways in which endangered species utilize habitats. The methods described here can only identify range locations in space, and cannot directly measure habitat selection or the relative importance of environmental factors on space use decisions by individuals or groups. Therefore, future studies should combine current range estimates with selection indices to indicate the factors limiting and influencing endangered species' distributions. Habitat or resource selection indices allow managers to model current and future species distributions, understand the potential impacts of ecosystem degradation and various management decisions, and conserve essential resources for endangered species (Millspaugh *et al.* 2006; Martinez-Meyer *et al.* 2006). Such indices may be particularly important in conservation decision-making for patchily-distributed species, and can aid in the identification and assessment of critical habitat both in and between current population patches (Harris *et al.* 2008). One range modeling method, the synoptic model of animal space use, couples home range models with resource selection to characterize the influences of environmental variables on species utilization distributions (Horne *et al.* 2008). Future studies should incorporate models like the synoptic space use model, to further our understanding of species range patterns, and inform conservation planning.

Tables

Table 1. Number of Cross River Gorilla Signs Observed for Each Month of Study Period

Month	Number CRG Sign Obs.
Jan-09	13
Feb-09	18
Mar-09	6
Apr-09	4
May-09	15
Jun-09	14
Jul-09	37
Aug-09	31
Sep-09	32
Oct-09	46
Nov-09	2
Dec-09	4
Jan-10	22
Feb-10	2
Mar-10	8
Apr-10	5
May-10	4
Jun-10	1
Jul-10	9
Aug-10	6
Total	279

Table 2. Area (km^2) and Cross Validation Criterion (CVC) for 50% Core Range Model Performance for Different Home Range Modeling Methods

Model	**Parameter**	**50 % area**	**95% area**	**99% area**	**CVC (Core)**	**ΔCVC**
r LoCoh	r = 1.4	4.72	18.93	24.29	373.1682	0
a LoCoh	a = 15	3.50	18.89	24.48	468.43	95.26
Grid Square	250 X 250 meters	2.19	7.88	8.56	484.005	110.84
K LoCoh	K = 33	3.29	23.73	26.80	502.2832	129.12
K LoCoh	K = 18	2.53	15.67	24.19	542.972	169.80
a LoCoh	a = 11.4	3.09	17.22	17.22	567.60	194.43
Grid Square	500 X 500 meters	4.00	16.75	19.75	582.7698	209.60
MCP		6.89	32.45	42.69	734.3855	361.22
Cluster		0.14	21.41	42.69	734.39	361.22
Fixed kernel	h = LSCV	2.08	9.48	13.25	937.8797	564.71
Fixed kernel	h = ad hoc	8.07	47.72	68.77	991.8447	618.68
r LoCoh	r = 0.8	2.42	13.01	13.09	1002.576	629.41
Fixed kernel	h = LCV	4.78	24.54	34.65	1261.32	888.15
Fixed kernel	h = half max nndist	9.44	54.24	78.59	1786.707	1413.54

Table 3. Comparisons of Subpopulation range Estimates with Subsampled (150 locations) versus Complete (279 locations) Data Set

Method	**Total Area (km^2)**	**Sub-Sampled Area (km^2)**	**% Locations inside sub-sampled range**	**Area Overlap (km^2)**	**% Area Overlap**
Cluster	43.38	42.22	96.06%	42.22	97.33%
MCP	43.41	42.22	96.06%	42.22	97.26%
K LoCoH	**31.73**	**31.63**	**98.21%**	**30.57**	**96.34%**
Kernel Density	47.72	42.58	99.28%	42.58	89.23%
a LoCoH	27.22	25.29	94.98%	22.81	83.80%
r LoCoH	13.09	10.38	90.68%	10.38	79.30%
Grid square (500 m)	20.25	15.25	92.11%	15.25	75.31%
Grid Square (250 m)	8.75	5.81	82.44%	5.81	66.40%

Figures

Figure 1. Minimum Convex Polygon Subpopulation Range Area Accumulation Curve

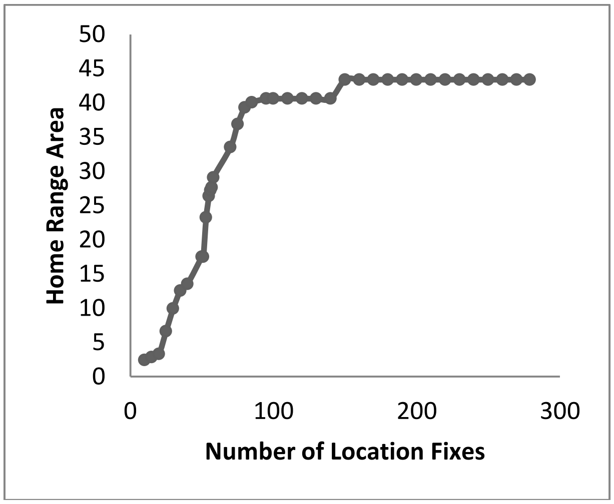


Figure 2. Subpopulation Range Size Estimates using Various Home Range Modeling Techniques.

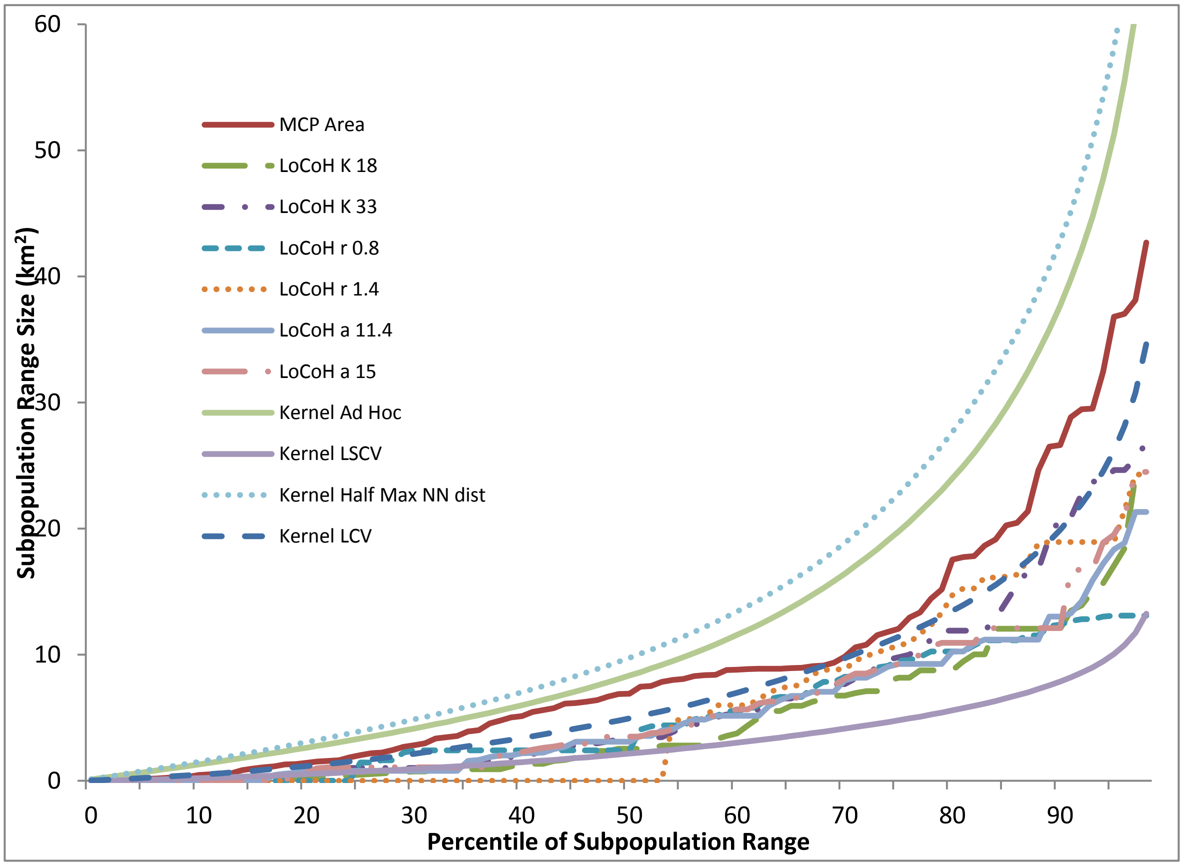


Figure 3. Minimum Convex Polygon Subpopulation Range Estimate

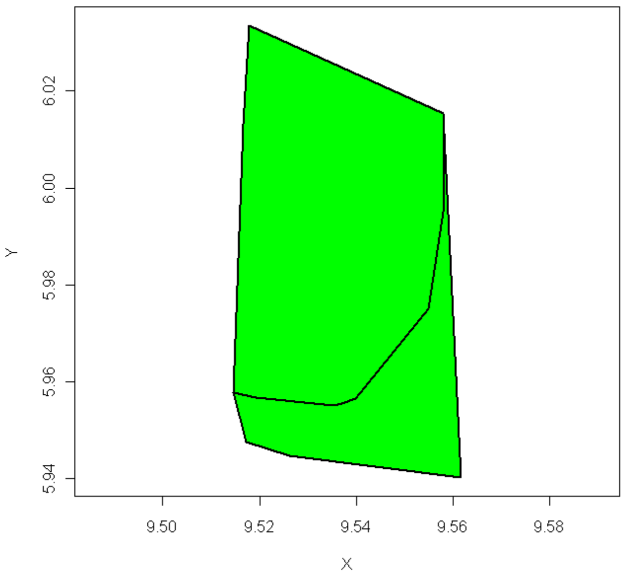


Figure 4. Grid Squares Subpopulation Ranges using 250 meter (a) and 500 meter (b) cell sizes

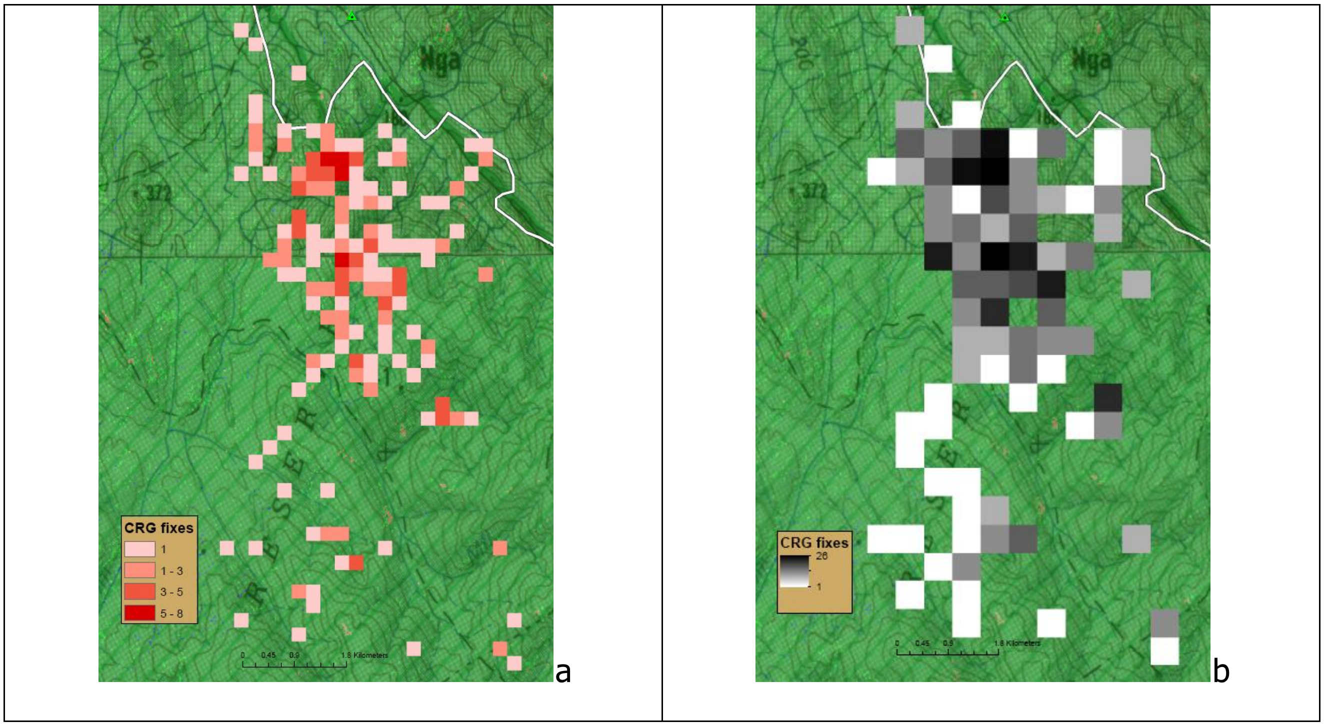


Figure 5: Kernel Utilization Distributions, with h (bandwidth) values calculated using ad hoc (a), half of the maximum nearest neighbor distance (b), least squares cross validation (c), and likelihood cross validation (d)

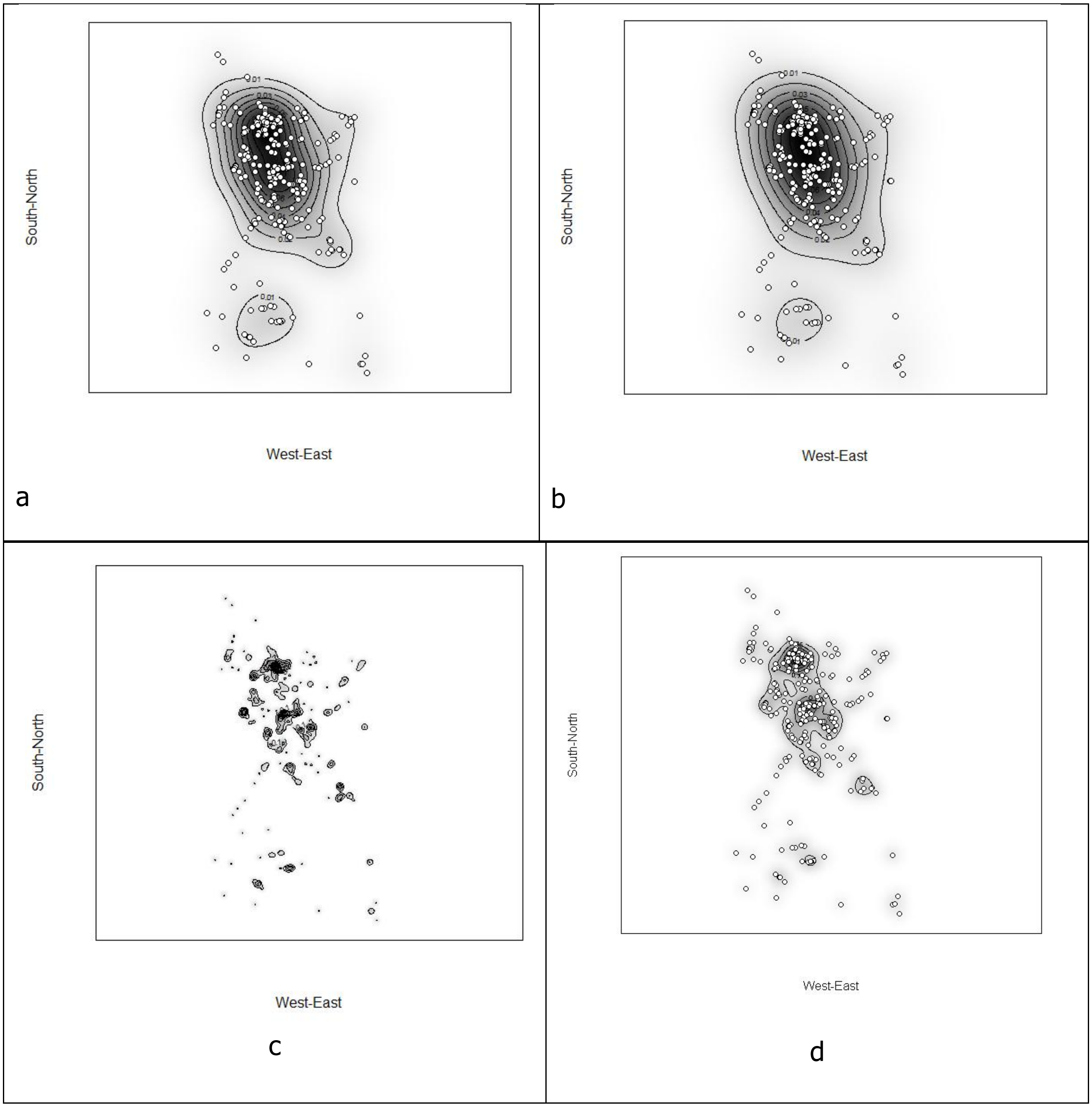
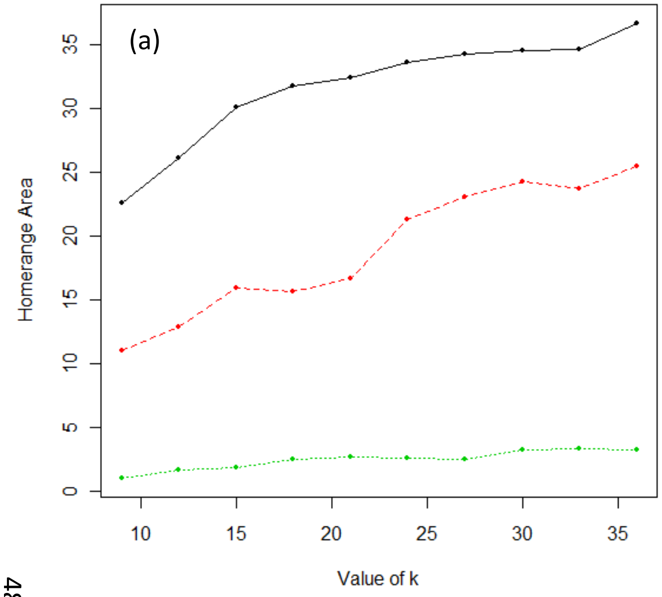
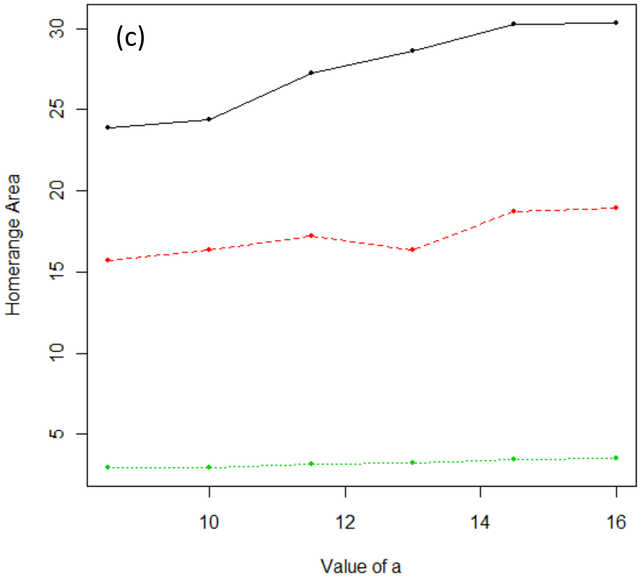


Figure 6.





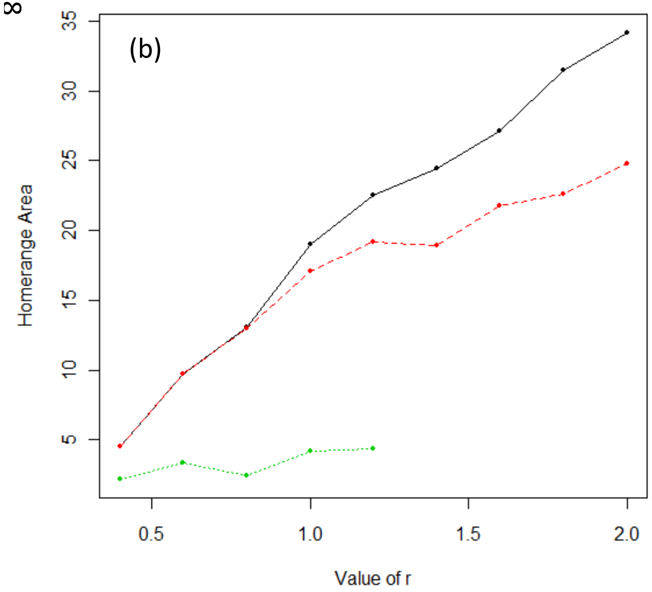


Figure 6(a) Range Area (100%, 95%, and 50%) versus Number of Nearest Neighbors (k)

Figure 6(b) Comparison of range area (100%, 95%, and 50%) for different search radii r

Figure 6(c) Comparison of areas of different Adaptive LoCoH values (11.4 km is the maximum distance between any two points in the dataset).

Figure 7(a). Comparison of four LoCoH Subpopulation Ranges, for varying K values

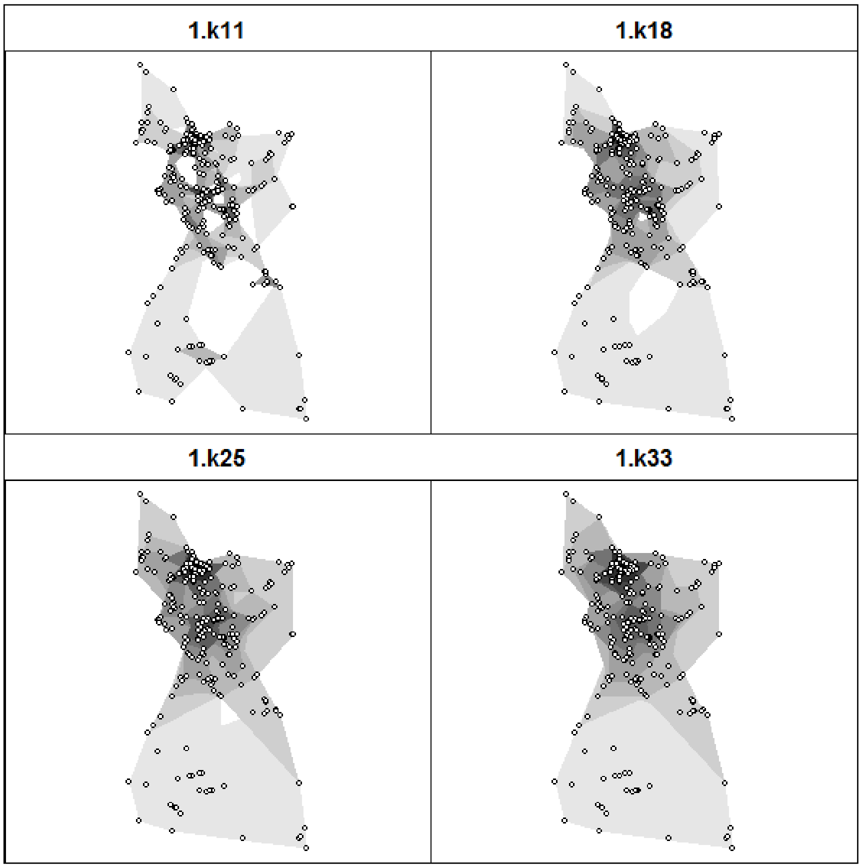
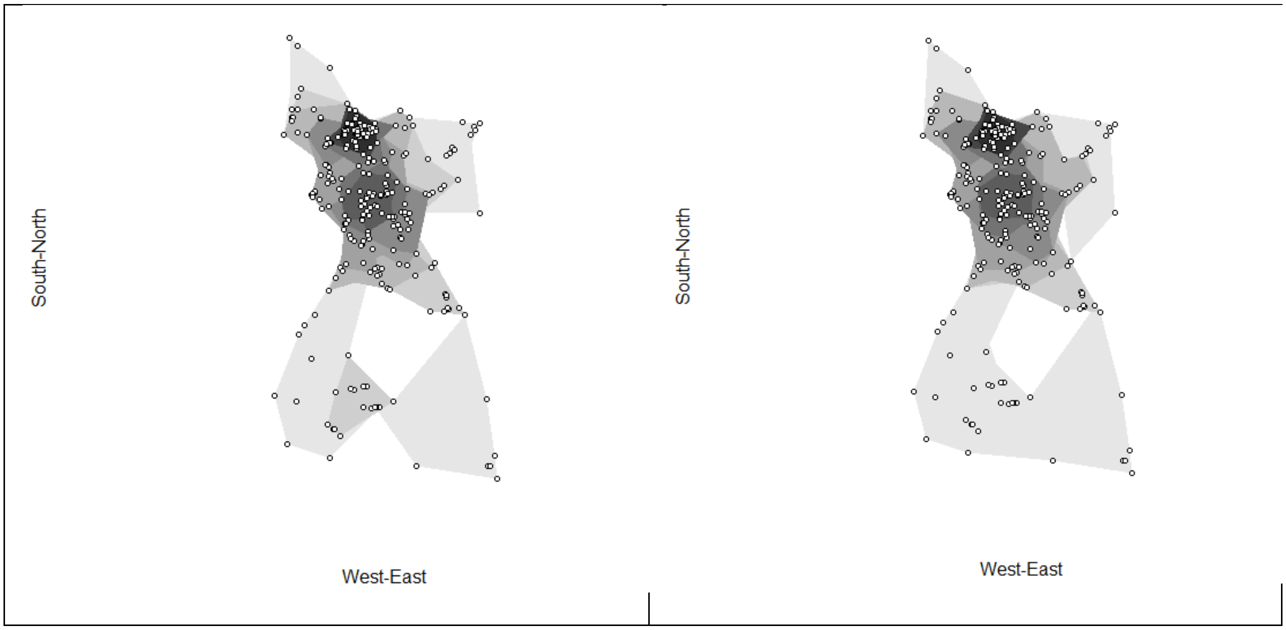


Figure 7(b) Fixed r LoCoH Subpopulation Ranges, r = 0.8 km (left) and 1.4 km (right)

Figure 7(c) Adaptive LoCoH Subpopulation Ranges, a = the maximum distance between points (left) and 15 kilometers (right).



CHAPTER 4:

Placing linkages among fragmented subpopulations: Do least-cost models reflect how animals use landscapes?

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Abstract

1. The need to conserve and create linkages among fragmented habitats has given rise to a range of techniques for maximizing connectivity. Methods to identify optimal habitat linkages face trade-offs between constraints on model inputs and biological relevance of model outputs. Given the popularity of these methods and their central role in landscape planning, it is critical that they be reliable and robust.
2. The most popular method used to inform habitat linkage design, least-cost path (LCP) analysis, designates a landscape resistance surface based on hypothetical ‘costs’ that landscape components impose on species movement, and identifies paths that minimize cumulative costs between locations.
3. While LCP analysis represents a valuable method for conservation planning, its current application has several weaknesses. Here, I review LCP analysis and identify shortcomings of its current application that decrease biological relevance and conservation utility. I examine trends in published LCP analyses, demonstrate the implications of methodological choices with our own LCP analysis for bighorn sheep *Ovis canadensis nelsoni*, and point to future directions in cost-modelling.
4. Our review highlights three weaknesses common in recent LCP analyses. First, LCP models typically rely on remotely-sensed habitat maps, but few studies assess whether such maps are suitable proxies for factors affecting animal movement or consider the effects of adjacent habitats. Secondly, many studies use expert opinion to assign costs associated with landscape features, yet few validate these costs with empirical data or assess model sensitivity to errors in cost assignment. Thirdly, studies that consider multiple, alternative movement paths often propose width or length requirements for linkages without justification.
5. *Synthesis and applications*. LCP modelling and similar approaches to linkage design guide connectivity planning, yet often lack a biological or empirical foundation. Ecologists must clarify the biological processes on which resistance values are based, explicitly justify cost schemes and scale (grain) of analysis, evaluate the effects of landscape context and sensitivity to cost schemes, and strive to optimize cost schemes with empirical data. Research relating species’ fine-grain habitat use to movement across broad extents is desperately needed, as are methods to determine biologically relevant length and width restrictions for linkages.

Key Words: Animal Movement, Connectivity, Corridor, Dispersal, Fragmentation, Linkage Design, Model Validation

Introduction

Habitat fragmentation and isolation have long been considered among the greatest threats to the persistence of species (Karieva 1987; Quinn & Harrison 1988). Fragmentation increases a species' risk of extinction from inbreeding and genetic and demographic stochasticity (Wilcox & Murphy 1985; Mills & Smouse 1994), and limits the ability of populations to move in response to perturbations (e.g. harvest, habitat degradation or disturbance). The effects of fragmentation on dispersal and colonization, in particular, have received increasing attention as planners attempt to predict the response of species to climate change (e.g. Thomas *et al.* 2004; McLachlan, Hellmann, & Schwartz 2007). Efforts to mitigate the impacts of habitat fragmentation by preventing or reversing population isolation are encompassed within the growing field of connectivity conservation (Crooks & Sanjayan 2006).

Promoting connectivity, the movement of species or genes between habitats, alleviates problems associated with habitat fragmentation (Crooks & Sanjayan 2006). Most efforts to conserve connectivity rely on the creation or protection of habitat linkages; i.e. land that promotes movement or dispersal of plants or animals between core habitats (Briers 2002; Beier, Majka, & Spencer 2008; Fig. 1). However, while researchers generally agree that maintaining connectivity is essential to the persistence of fragmented subpopulations, they often disagree on the process by which linkages are designed for conservation (Rothley 2005). Though placement of linkages/corridors based on empirical observations of dispersal movement may be the most reliable method for designing connectivity networks (Hilty & Merenlender 2004; Graves *et al.* 2007), such data are sparse or non-existent for most species and most locations (Fagan & Calabrese 2006). As a result, conservation relies heavily on models of connectivity that may have little empirical basis. Conservation planners are faced with a critical question: will such models improve placement of linkages/corridors by explicitly incorporating habitat effects on movement, or will they result in misleading and potentially costly recommendations for conservation by concealing invalidated assumptions (Chetkiewicz, St. Claire, & Boyce 2006)?

In this review, I evaluate the current use, strengths, and weaknesses of least-cost path (hereafter 'LCP') analysis (Fig. 1; see appendix 4 for a discussion of current least-cost path terminology), the most widely used modelling approach for design of habitat linkages (LaRue & Nielsen 2008; Phillips, Williams, & Midgley 2008). I focus on applications of LCP analysis in which a single path or corridor is identified for placement between pairs of source patches. A detailed description of the steps involved in LCP analysis is provided in Figure 1. In short, LCP analysis evaluates potential animal movement routes across the landscape based on the cumulative 'cost' of movement

(Chetkiewicz & Boyce 2009). Resistance of each landscape unit (usually a grid cell on a raster map) is intended to represent the sum of hypothetical energetic expenditures, mortality risks, or other facilitating or hindering effects of landscape elements on movement within the cell (Adriaensen *et al.* 2003; Fig. 1). In practice, resistance values in LCP models are usually assigned on an arbitrary scale meant to reflect 'high' or 'low' suitability (with respect to movement) of different landscape factors (e.g. land cover, human activity, etc.). Resistance values for each factor are weighted according to their perceived importance and combined (e.g. by geometric mean) to produce a single resistance value. I call this series of choices the 'cost scheme'. The 'effective distance', or cost of a path between habitat patches for a species, is the Euclidian distance weighted by the cumulative resistance values of all cells traversed (Adriaensen *et al.* 2003; Beier, Majka, & Spencer 2008; Fig. 1). The LCP is the combination of cells that minimizes effective distance between two patches (Verbeylen *et al.* 2003) and is used to inform optimal placement of a linkage (Fig. 1).

LCP analysis is an attractive technique for analyzing and designing habitat corridors because it: i) allows quantitative comparisons of potential movement routes over large study areas, ii) can incorporate simple or complex models of habitat effects on movement, and iii) offers the potential to escape the limitations of analyses based solely on structural connectivity (i.e. designating areas simply as 'patch', 'matrix' or 'corridor') by modelling connectivity as it might be perceived by a species on a landscape ('functional connectivity'; Taylor, Fahrig, & With 2006). However, as with any modelling approach, the effectiveness of LCP analysis is limited by the quality of input data. For instance, modellers often use expert opinion to assign resistance values to remotely-sensed landscape traits (e.g. Adriaensen *et al.* 2003; see Fig. 1 & Table 1). Thus, the accuracy and value of these models depends on how strongly these coarse-grain habitat proxies and their assumed resistances correlate with actual habitat use/movement by focal species (Calabrese & Fagan 2004; Beier, Majka, & Spencer 2008). Methods for defining habitat patches are often unclear or based largely on human rather than animal perception of habitats (Theobald 2006). In worst-case scenarios, LCP analyses are little more than subjective interpretations of coarse habitat maps, but the method has potential for much more. For example, ideal applications of LCP analysis would employ organism-centric approaches in which practitioners use species- and landscape-specific empirical data to quantify behavioural responses to finer-grain habitat elements (e.g. distribution of critical resources, escape cover and threats), to a) consider attributes of surrounding cells when assessing resistance of a cell, and b) assess the likelihood of use for a path of known width and length (Adriaensen *et al.* 2003; Theobald 2006; Graves *et al.* 2007). While a challenging standard, such organism-centric approaches have the potential to reduce researcher bias and increase the replicability, defensibility, and transparency of LCP and related analyses (Chetkiewicz & Boyce 2009).

In reviewing the use and application of LCP approaches I set out to address the following questions: 1) Do recent studies employing LCP analysis shift emphasis from structural towards functional connectivity by considering species-specific behaviours and do they provide explicit, empirically derived justification for their choices? 2) Do researchers using LCP analysis attempt sensitivity analysis, model validation, or compare multiple model outputs to assess the robustness of their projections? 3) How have researchers translated LCP model outputs into optimal linkage or corridor placement for their study areas?

Last, to demonstrate the challenges of LCP analyses and highlight the sensitivity of LCP model outputs to input data, I present a case study in which I conduct an LCP analysis for desert bighorn sheep *Ovis canadensis nelsoni* (Merriam 1897) in Southern California. I use our LCP analysis between two bighorn populations to examine congruence of outputs from two commonly used techniques for assigning cost schemes (expert opinion and gene flow optimization; see Figs. 1 & 2) and two scales of habitat suitability assessment (regionally-significant topographic/anthropogenic variables and locally-specific habitat traits).

Materials and methods

Selection of papers

We limited our analytical review to studies with the stated aim of designing optimal connectivity strategies for focal species. I performed a search in ISI Web of Knowledge (ISI 2010) using the following search terms: *least-cost* OR *cost-distance* OR *least-cost path* OR *least-cost-path* AND *connectivity* OR *corridor* OR *linkage* OR *conservation.* To reflect current trends in the peer reviewed literature, I restricted my search to 373 studies published between 2002 and 2010. I then refined the list to the subject areas Biodiversity and Conservation, Environmental Sciences and Ecology, and Genetics and Heredity, which reduced our pool to 135 results. I then further restricted the review to publications with the following key words in the study abstract: *identify* OR *predict* OR *model* OR *delineate* OR *place* OR *validate* OR *draw* AND *linkage* OR *corridor* OR *optimal connection* OR *key connectivity area* OR *migration zone.* I excluded studies that used LCP analysis solely to predict occupancy, model species distributions (e.g. Verbeylen *et al.* 2003; Magle, Theobald, & Crooks 2009), explain gene flow (e.g. Vignieri 2005), or predict how landscape changes might affect focal species (e.g. Graham 2001) if they did not explicitly aim to design or evaluate linkages. Finally, for each study that met our criteria for inclusion, I evaluated the following methodological choices: type of habitat data, choice of grain (cell size) and study extent, determination of cost-schemes and source patches, consideration of effects of adjacent habitat, exploration of different resistance values, sensitivity analysis for other modelling choices and conversion of a ‘path’ to a ‘corridor’.

Bighorn sheep case study

To test the sensitivity of LCP model outputs to input data, I compared two LCP models published for bighorn sheep populations in the Mojave Desert of California (Epps *et al.* 2007; Penrod *et al.* 2008), and two additional LCP models based on modifications of those published models. I chose two populations, San Gorgonio and Cushenbury, that exhibit clear evidence of connectivity in the recent past (Epps *et al.* 2010).

The 'Expert' model (Penrod *et al.* 2008) was based on a linkage design for nearby Joshua Tree National Park. The Expert model estimated resistance values using expert opinion and included dense woody vegetation as determined from the California Wildlife Habitat Relationship vegetation type (Mayer & Laudenslayer 1998). Areas of flat topography, urban areas, and areas with high road density were all defined as highly resistant (up to 10 times more than the best habitat). The final combined model was calculated as:

$$\text{Cost}_{\text{EXPERT}} = \text{topography}*0.4 + \text{habitat}*0.4 + \text{road density}*0.2$$

where topography, habitat, and road density were assigned resistances between 1 and 10, as specified by Penrod *et al.* (2008, pp. 7-10).

The 'Optimized' model (Epps *et al.* 2007; Appendix 2) considered only topography and optimized resistance values using observed gene flow among populations over the entire study area, including those in our case study:

$$\text{Cost}_{\text{OPTIMIZED}} = \text{topography}$$

where areas with >15% slope and <15% slope were assigned resistances of 1 and 10, respectively.

Epps *et al.* (2007) recognized that their model was optimized for the southern California population as a whole, and would not account for locally-specific habitat variables, such as the large amount of wooded habitat in the vicinity of the San Gorgonio and Cushenbury populations. Bighorn sheep typically avoid wooded habitat, presumably because of higher predation risk (e.g. DeCesare and Pletscher 2006). Therefore, I developed a third model ('Optimized Local') that added high resistance for any urban area (10 times higher) or wooded area (10 times higher) and calculated the final model as:

$$\text{Cost}_{\text{OPTIMIZED LOCAL}} = \text{topography}*0.33 + \text{wooded habitat}*0.33 + \text{urban area}*0.33$$

where areas with >15% slope and <15% slope were assigned resistances of 1 and 10, respectively, wooded habitat was assigned a cost of 10, and urban habitat was assigned a cost of 10. Non-wooded and non-urban areas were assigned a cost of 1.

Finally, to simulate the common situation where little is known about dispersal, I constructed a fourth model ('Incomplete') that was biologically relevant but omitted several important factors:

$\text{Cost}_{\text{INCOMPLETE}}$ = wooded habitat

where areas with and without tree cover were assigned a cost of 10 and 1, respectively.

All input grids were re-sampled to 100 metre resolution before combining into final cost grids. I calculated a single LCP for each model using Pathmatrix (Ray 2005). I used ArcMap and CorridorDesigner (http://www.corridordesign.org/) to generate 'least-cost corridors' (Beier, Majka, & Newell 2009; Fig. 1) representing the lowest 10% of possible least-cost paths for each model and estimated the area of overlap of those least-cost corridors.

Results

Literature review

Twenty-four studies met our criteria for review. Each of the 24 used remotely-sensed land-cover or habitat type as a proxy for habitat suitability and movement of focal species (Table 1). Study extent ranged from 10- 4,000,000 km^2; and study grain (cell size) varied from 1 m^2 to 1 km^2 but most commonly corresponded with the grain of freely-available Landsat imagery (900 m^2; see Appendix 5 for a complete summary of reviewed studies' methodological choices). Two studies distinguished only two types of habitat while all others included at least three habitat categories (Table 1). None of the 24 studies directly considered more organism-centric measures of microhabitat suitability, including those identified by authors as affecting animal habitat selection/movement, such as percentage habitat-cover or distribution of food (Binzenhofer *et al.* 2005), presence of nutrient sources such as salt-licks (Beazely *et al.* 2005), denning/nesting habitats (Singleton, Gaines, & Lehmkuhl 2004), prey availability (Rabinowitz & Zeller 2010), or cover or escape terrain for predator avoidance (Wang *et al.* 2008). While some studies stated that habitat types serve as reliable proxies for predator presence and/or abundance of preferred foods (e.g. Driezen *et al.* 2007; Shen *et al.* 2008), no studies validated this assumption or included habitat distribution models of either predator or prey species.

Fourteen of the 24 studies evaluated in our review based their LCP analysis cost schemes (Fig. 1) on expert opinion, published literature, or both, although explanations of cost surface derivation were often lacking in sufficient detail to replicate analyses (Table 1). Of those, only three attempted to systematically and objectively translate expert opinion into cost schemes (e.g. using Analytic Hierarchy Process or similar approaches (Banaikashani 1989; see Appendix 5). Six studies used telemetry or trapping (presence) data to designate costs. Three studies used relative gene flow, or combined gene flow and telemetry data, and two studies assigned resistance values using behavioural data from focal species. Across the surveyed studies, source habitat patches were variably defined as 'known population/individual locations' (10 studies), habitat deemed most 'suitable' by size, habitat type, or both (nine studies), or 'key conservation areas' (one study). Four studies did not define their source patches (Table 1). Eight studies included some effect of surrounding habitat in their cost designation (Table 1). Six studies partially based pixel cost on distance to particular habitat types or human activities. Kindall & Van Manen (2005) included forest/agriculture edge density in their cost measures while Wikramanayake *et al.* (2004) considered all areas within 1 km of agriculture or population centres to be 'poor habitat', regardless of habitat type.

Only four studies (17%) quantitatively assessed sensitivity of model-selected paths to *different* cost schemes for all variables, and these four consistently found their model outputs to be highly sensitive to input decisions (Table 1). Larkin *et al.* (2004) found overlap of only 0-51% among paths generated using different cost schemes. Stevens *et al.* (2006) and Epps *et al.* (2007) used multiple measures of gene flow to test LCP models and discovered that models were highly sensitive to different resistance values. Driezen *et al.* (2007) showed that the measurement of a species' ability to find low-cost sites depends heavily on the cost scheme used. Three other studies conducted partial sensitivity analysis: Schadt *et al.* (2002) found that changing resistance values of the matrix led to significantly different LCPs while Shen *et al.* (2008) discovered high model sensitivity to costs of bamboo and land cover. Kautz *et al.* (2006) did not detect model sensitivity to costs of roads and water. Only nine of the 24 studies attempted some form of model validation in the published results (Table 1). Four studies examined relative support for cost schemes based on gene flow. Four studies used presence data (telemetry or trapping) to validate their models, while one used presence and absence data (Beazley *et al.* 2005).

Only 10 of the 24 studies I evaluated attempted to move beyond a single-pixel wide path to consider more biologically-relevant (Majka, Jenness, & Beier 2007) least-cost corridors (LCC; see Fig. 1) either by including minimum acceptable widths, buffering paths, or selecting a percentage of least-cost cells (Table 1). Two studies included a minimum acceptable width cut-off. Kautz *et al.* (2006) found that one-pixel wide paths can go through extremely unsuitable habitat, and therefore buffered LCPs and rejected paths that passed through poor-quality habitat types. Four additional studies buffered their LCPs to make them wider. Three studies took a percentage of lowest grid cell values to make a least-cost corridor. However, empirical justifications for most of these analytical choices, such as buffer width, were not presented when defining LCCs.

Case study: least-cost path analysis of bighorn sheep

The four LCP models compared in our analysis of two populations of desert bighorn sheep produced LCPs that varied widely in location and length (Fig. 2). Along-path distances for the four paths were 34.6 km (Expert), 21.6 km (Optimized), 31.7 km

(Optimized Local), and 28.5 km (Incomplete); those paths overlapped <2% of total length (Fig. 2). Least-cost corridors overlapped from 0-44% (average 13%; Table 2).

Discussion

Literature review

Though LCP modelling has been touted as combining detailed geographical information with animal behaviour to move beyond structural towards functional connectivity analysis (Adriaensen *et al.* 2003; Theobald 2006), our review suggests current LCP model implementation often ignores factors that affect how animals utilize landscapes. Nearly all recent LCP analysis-based studies employed coarse-grain environmental data layers to determine habitat connectivity, an approach that is often biased by researcher-perceived structural connectivity and runs the risk of missing important biological aspects of species' connectivity (Mortelliti & Boitani 2008). For instance, though scale of analysis has been shown to greatly impact strength of detected relationships, study grain was typically dictated by freely available remotely-sensed data (see Appendix 5) rather than species perceptions of landscape features (Cushman & Lewis, 2010; see Appendix 3 for recommendations on improving application of LCP analysis).

Overall, the strength of the correlation between remotely-sensed habitat layers and species' movement is relatively unknown and poorly validated (Chetkiewicz, St. Claire, & Boyce 2006; Beier, Majka, & Spencer 2008). Our analysis in no way rejects the utility of coarse proxy data, especially given the need to model movement over large landscapes, but illustrates the need to explore effects of scale, explicitly justify choice of scale, and conduct model sensitivity and validation (see Appendix 3). In many cases, remotely-sensed proxies may provide adequate coverage at limited cost, and may prove to be efficient for conservation planning in the face of limited time and funding (e.g. fishers (*Martes pennanti*): Caroll, Zielinski, & Noss 1999; large carnivores: Schadt *et al.* 2002; bighorn sheep: Epps *et al.* 2007). However, animals frequently select high quality microhabitats in areas that appear unsuitable at a macro-level (Mortelliti & Boitani 2008). Animals often select against low quality habitat within largely suitable areas as well, and accounting for the presence of low quality habitat within otherwise high quality habitat patches may significantly improve model predictions (e.g. Wang *et al.* 2008).

We suggest that those using LCP analysis should strive to evaluate predictive power of coarse-grain proxies for focal species movement over a portion of the study range before constructing analytical models (see Appendix 3). For species and linkages above the scale of rapid dispersal movements, using resource selection function models (RSF) with LCP analysis appears to be a step forward from more arbitrary methods (e.g. Chetkiewicz & Boyce 2009). Hypothesis testing and model selection that compares critical scales of habitat-use or movement for taxa will help to build a stronger foundation for linkage-design methodology. Better understanding of a species' perception of its environment will help modellers to identify appropriate scales of analysis and, thus, provide more reliable and accurate model outputs for practitioners (With, Gardner, & Turner 1997; Uezu, Metzger, & Vielliard 2005; Cushman & Lewis 2010).

Least-cost path analysis of bighorn sheep

Our LCP analysis of bighorn sheep in California demonstrated many of the challenges and uncertainties I highlight above. The four models used to identify LPCs for desert bighorn sheep were derived at different scales (e.g. metapopulation versus population level) and yielded very different paths (Fig. 2). Use of 10% least-cost corridors for each scheme did little to reduce differences between the models (Fig. 2, Table 2). For instance, the corridor suggested by the Optimized model (developed over a much larger geographic area) did not overlap with the Optimized Local model, which included wooded and urban habitat (Fig. 2). The Optimized model only partly overlapped the Expert model corridor, which was based only on coarse habitat maps and expert opinion (Fig. 2). This case study makes clear that reasonable alternative models can lead to strikingly different conclusions regarding prioritization of land acquisition, easements or other management actions for linkage conservation.

How can we improve least-cost path modelling?

Organisms respond differently to landscape elements depending on their perceptive range and characteristics of surrounding areas (Coulon *et al.* 2008; Richard & Armstrong 2010). Species' movements in one habitat type will often be affected by nearby disturbances such as man-made structures and light pollution (Coulon *et al.* 2008; Beier 1995), width of habitats (Laurance & Laurance 1999; Hilty & Merenlender 2004), traits of and distance to adjacent habitat (Binzenhofer *et al.* 2005; Anderson, Rowcliffe, & Cowlishaw 2007; Richard & Armstrong 2010), and level of perceived cover and safety (Rizkalla & Swihart 2007; Beier, Majka, & Spencer 2008). However, only two of twenty-four studies in this review were able to validate their model with behavioural data (Stevens *et al.* 2006; Driezen *et al.* 2007). Given the sensitivity of least-cost models to incorrect resistance specification, the best way to evaluate model performance would be comparison of predictions based on multiple methods and independent data sets (e.g. radiotelemetry movement data and landscape genetics: Cushman & Lewis 2010). Testing the role of individual behaviour, preference, and perceptual range in habitat-selection or movement decisions (e.g. radio or global positioning system tracking: Beier 1995; Cushman, Chase, & Griffin 2010; Driezen *et al.* 2007; Richard & Armstrong 2010; experimental data: Stevens *et al.* 2006; Hadley &

Betts 2010) and using model selection to better integrate these behavioural with ecological and landscape data will greatly improve connectivity design (see Appendix 3). Additionally, using hierarchical resource selection functions to understand habitat use, movement, and behavior at multiple scales will help inform better LCP modeling.

Determining the relationship between movement or gene flow and effective distance under a given cost scheme, and thus the maximum effective distance at which a corridor is useable by a given species, may be the most biologically important and widely ignored aspect of LCP and other connectivity analyses. Even the best-supported paths will not function as planned if their lengths exceed the movement capability of a focal species. For example, gene flow estimates (Epps *et al.* 2005; 2007) suggest that in our bighorn sheep example, only the corridors produced by the Optimized and Incomplete models would serve a connective function (21.6 and 28.5 km along-path lengths, respectively) while the Expert and Optimized Local models would result in corridors too long to promote connectivity (35 and 31.7 km respectively). Yet only two studies reviewed here (Schadt *et al.* 2002; Singleton, Gaines, & Lehmkuhl 2004) considered cut-offs for maximum useable effective distance (the greatest effective distance a species can travel between patches) based on knowledge of species dispersal. One study used gene flow estimates to determine maximum effective distance (Epps *et al.* 2007; Appendix 2). I recommend that wherever possible, defensible estimates of maximum useable effective distance should be developed by analyzing genetic or movement data as functions of effective distance (see Appendix 3). An alternative approach is to define resistance more explicitly in terms of biological parameters, such as mortality risk or energy expenditure based on demographic, diet, or metabolic data, and use movement models based on those parameters to explore modelling choices (see Chetkiewicz, St. Claire, & Boyce 2006). In general, a more explicit discussion of resistance in each study would improve linkage design and interpretation. For instance, does the resistance value used in an LCP analysis reflect the physical costs of moving through a cell, its mortality risk, or habitat value? Each definition may be defensible depending on the goals and scale of analysis, but each will have different implications, especially when considering maximum path lengths.

Individual animals rarely use a single optimum route, and single-pixel-wide LCPs are of limited biological value (Majka, Jenness, & Beier 2007; McRae & Beier 2007; McRae *et al.* 2008; Pinto & Keitt 2009). Although alternative paths with comparable costs may exist on a landscape, studies regularly failed to consider larger swaths of low-cost grid cells (i.e. a least-cost corridor). Recently, circuit theory has been used to incorporate multiple pathways and patch characteristics when evaluating connectivity designs (McRae & Beier 2007; McRae *et al.* 2008). This method allows modelling alternative linkages, ranking potential corridors, and reassigning values as pathways are removed (Fig. 1; see Appendix 3), but it is equally reliant on a biologically-realistic resistance surface. Alternatively, researchers can select lowest percentiles of cost surfaces (Beier, Majka, & Newell 2009; this study Fig. 2) or combine multiple low-cost routes in an LCP analysis to delineate ‘probable movement zones’ (Rayfield, Fortin, & Fall 2010; see Appendix 3). While these alternatives may increase robustness to uncertainty in model parameters, selection of a percentile cut-off (e.g. lowest 10%) or combining a number of low-cost routes is still a subjective decision with unclear biological justification. Some of the techniques I describe above for optimizing or validating models of effective distance should also be applied to this problem.

Few studies examined in this review conducted sensitivity or uncertainty analyses, which are essential to the landscape planning process and should be a requirement of any LCP or related connectivity model (Beier, Majka, & Newell 2009; Rayfield, Fortin, & Fall 2010). Studies that conducted sensitivity analyses (Table 1) found that different cost schemes (both choice of factors incorporated in the resistance surface, as well as the weights and resistance values assigned) produced very different LCPs, although Beier, Majka, & Newel (2009) found their models robust to uncertainty. Indeed, Beier, Majka, & Newel's (2009) methods for evaluating uncertainty should prove useful where data for optimizing cost schemes are sparse (see Appendix 3). Sensitivity to the choice of habitat factors, factor weights, resistance values, grain, and definitions of least cost corridors should all be considered (see Appendix 3). Our LCP analysis for desert bighorn sheep highlights the disparity of LCPs based on expert opinion, gene flow optimization models, and other reasonable combinations, as well as the point that models optimized over large areas may still need local modifications. Researchers should strive for replicability, objectivity, and organism-centred methodology to improve efficacy of LCP and other models in connectivity conservation planning (see Appendix 3). To avoid accusations of 'black-box' modelling (e.g. Shrader-Frechette 2004), studies must clearly address details of model construction, assumptions, and uncertainties. Resource selection functions optimized at multiple scales will aid in clarifying model construction. Through these improvements, connectivity science will more ably inform landscape planning.

LCP analysis and other connectivity conservation approaches should be viewed as one piece of a larger landscape conservation puzzle. Least-cost modelling cannot fully incorporate quality, size, or importance of individual source patches, thus, it is best applied as part of a wider conservation strategy for focal species. A current debate questions whether connectivity conservation strategies like LCP analysis bear consideration in conservation planning, or simply detract focus from more certain measures to protect high-quality breeding habitats (Hodgson *et al.* 2011; Doerr, Barrett, & Doerr 2011). This debate promotes a dichotomy between high-quality breeding habitat and habitats designated for connectivity that may represent an overly simplistic view of connective habitats. Regardless, recent summaries (e.g. McLachlan, Hellmann, & Schwartz 2007; Hodgson *et al.* 2011) emphasise that conservation of diverse and connected habitat mosaics is likely to be the safest approach for sustaining species on our rapidly changing planet.

Table 1. Summary of recent studies that used least-cost path (LCP) modelling for habitat connectivity design (see Appendix 5 in Supporting Information for a more complete summary)

Study	**Variables Included**[1]	**Source of Cost Scheme**[2]	**Source Patches**[3]	**Adjacent habitat**[4]	**Cost Value Ranges**	**Validation**	**Sensitivity Analysis**	**Path to Corridor**[5]
Beazley *et al.* 2005	Forest cover (3); road density	EO; L ; HSI; S	All 'suitable' habitat patches (HSI)	No	Unknown	Presence / absence of dung	No	Minimum width
Chetkiewicz & Boyce 2009	LCT (5); sub-region; food resources; terrain; road density	RSF; RT	High RSF value polygons	No	Inverse of RSF coefficients	Telemetry locations;	No	Buffered: 350 meters
Cushman, McKelvey, & Schwartz 2008	LCT (26); elevation; slope; roads	EO; L; G	Individual locations;	No	1-10	Genetic distance	No	Smoothed: 2500 m radius parabolic kernel
Driezen *et al.* 2007	LCT (12); roads; water	L; PS	Unknown	No	1 - 1000	Experimental dispersal data	Compared 12 sets of costs	No
Epps *et al.* 2007	Slope (2); distance; barriers	G; RT	MCP; suitable habitat; EO	No	0.1-1.0	Radio-telemetry data	Compared multiple gene flow measures	No
Hepcan *et al.* 2009	VT (12); road density	EO; L	'Key Biodiversity Areas'	No	Unknown	No	No	Minimum width: 1 km

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[1] LCT: Land Cover Type, LUT: Land Use Type; HT: Habitat Type; VT: Vegetation Type. NDVI: Normalized Difference Vegetation Index. Number of cover/type categories is indicated in parentheses

[2] L: Literature; EO: Expert Opinion; RT: radiotelemetry; G: genetics; S: species presence locations; PS: Previous Studies HSI: habitat Suitability Index; RSF: Resource Selection Function

[3] HR: Home Range; MCP: Minimum Convex Polygon

[4] Did study consider adjacent habitat characteristics when determining resistance of cell?

[5] Did study go beyond least-cost path (LCP) to make a more biologically relevant recommendation, or least-cost corridor (LCC)?

Joly, Morand, & Cohas 2003	HT (7); roads; rivers	EO; L	Unknown	No	HT: 5-80; roads: 0-1	No	No	No
Kautz *et al.* 2006	LCT (16)	RT	HR & potential habitats (HSI)	No	LCT: 1-11; water: 15; road: 20	No	Partial: road & water	Post-analysis buffer
Kindall & Van Manen 2007	Forest cohesion, diversity, forest-agricult. edge density	Prob. of occurrence model	50% fixed kernel HR	No	1 -8	No	No	No
Kong *et al.* 2010	LUT (12)	EO	Urban green space >12ha connected to areas outside city	No	0.1 - 50,000	No	No	No
Larkin *et al.* 2004	HT (5) based on suitability model	EO; L	'Suitable' habitat (EO)	No	1 ; 10; 50; 100	No	Two cost schemes	No
LaRue & Nielsen 2008	LCT (8); dist. to road & water; slope, human pop. density	EO	Areas where cougar may be living (EO)	Distance to road & water	0.19 - 1.92	No	No	Buffered LCP by 1 km
Li *et al.* 2010	LCT (9), slope; dist to water & human activities (3)	EO	Panda occurrence or suitable habitat	Distance to human activities	Reciprocal suitability: 0.002 - 0.098	No	No	Smoothed: 90 m cumulative kernel
Meegan & Maehr 2002	HT (2); roads	EO; L; RT	forest patches ≥500 hectares	No	1,2, or 3	presence locations	No	No

Osborn & Parker 2003	HSI (2); dist. to river, roads, & settlements	EO	Individual locations	Dist. to settlement & road	Unknown	No	No	No
Rabinowitz & Zeller 2010	LCT; % tree/shrub cover; elev.; dist. to road & settlement; human pop. density	EO	Jaguar conservation units	Dist. to road & settlement	Integers 0-10	field interviews on-going	No	Selected lowest 0.1% of grid cell values
Rouget *et al.* 2006	'Suitability' (foraging model)	Unknown	Unknown	No	0; 300; 600; 900	No	No	Buffered to 1 km
Schadt *et al.* 2002	LCT (5); roads	EO; L	'Suitable' habitat: size, isolation, & forest cover	No	1 - 1000	No	Partial: 'matrix'	No
Shen *et al.* 2008	LC; bamboo cover; slope, elev; aspect; dist. to road & residential areas	EO	'Core' habitats based on LCT	Dist. to residential area & road	1-50	No	Partial: land & bamboo cover	No
Singleton, Gaines, & Lehmkuhl 2004	LCT (13); road density; human pop. density; slope	EO; L	Largest areas of low human influence with suitable LCT	No	0.1-1.0	No	No	Selected lowest 10% of cost surface
Stevens *et al.* 2006	LCT (6); water	Movement behaviour	Population MCP	No	3 Models: 1-10000	Genetic dispersal rates	Compared multiple gene flow measures	No

Wang *et al.* 2008	NDVI; slope; aspect; dist. to LCT	HSI on S	Individual locations	Distance to LUT	1-1,000	Presence; Gene flow	No	No
Wang, Savage, & Shaffer 2009	VT (3)	EO; S	Breeding pair locations	No	1-10	Gene flow estimates	No	No
Wikramanayake *et al.* 2004	HT (3); elev.; LCT in buffer (5); patch size	EO; PS	Unknown	Dist. to agriculture or pop. centre	1-25	No	No	Selected 10, 20, & 30% of lowest cost cells

Table 2. Percentage overlap of least-cost corridors based on four connectivity models between two bighorn sheep populations.

Model	Incomplete	Expert	Optimized
Expert	0%		
Optimized	5%	44%	
Optimized Local	30%	0%	0%

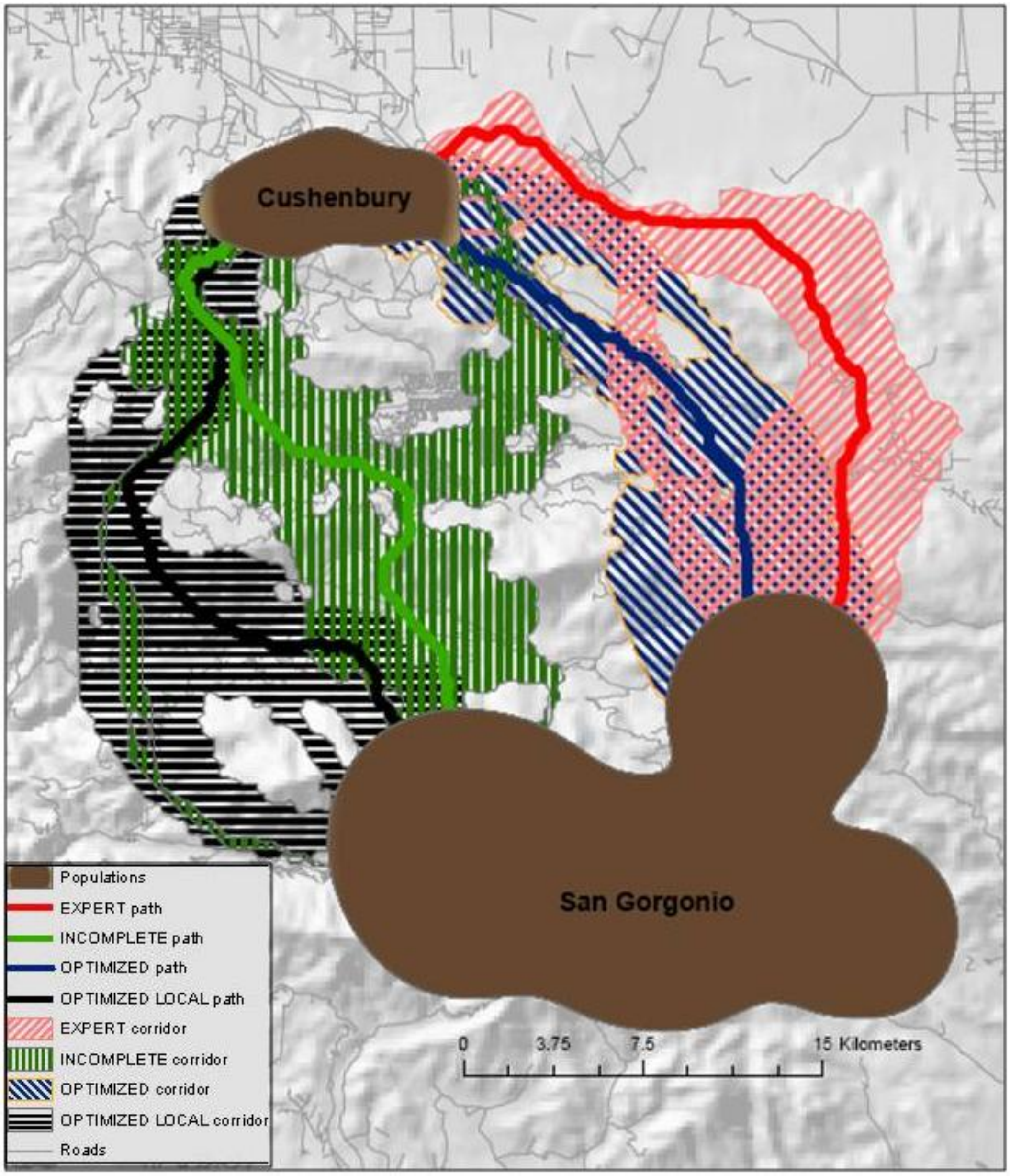
Figure 1.

Legend: Introduction to important questions, steps, and definitions for least-cost path modelling

Question	What areas need to be connected?	What landscape traits affect species' movement between these areas?	How will variation in these landscape traits affect animal movement?	How can these potential landscape effects be quantified?	To what degree does the landscape facilitate or impede movement between patches?	What is the easiest travel route between identified patches?	How can a least-cost path be translated into an optimal linkage?
Analysis	**Determine Source Pathces**	**Identify landscape variables to include in cost analysis**	**Rank variables according to resistance to movement**	**Develope cost scheme: assign resistance values and factor weights**	**Calculate cumulative cost surface from source patches**	**Identify least-cost path (LCP) between source patches**	**Design least-cost corridor (LCC)/ linkage (LCL)**
Definitions	**Source Patches**: Areas that support or have potential to support the species of interest; sometimes restricted to breeding habitat	**Landscape Variables**: Habitat traits *perceptible* by- and *likely to influence* – species' movement ➢ e.g. vegetation type, slope, elevation, water, human activities, food availability, escape cover	**Resistance**: A measure of reluctance to use habitat for movement (Adriaensen *et al.* 2003) or failure to move successfully	**Cost Scheme**: Choice of resistance values & factor weights **Resistance value**: numerical score assigned to habitats or landscape traits to quantify resistance **Factor weight**: measure of importance of one habitat trait on movement decisions *relative* to other traits	**Effective distance**: Composite measure of connectivity between patches representing geographic (Euclidian) distance weighted by resistance of landscape elements traversed on a given path (Adriaensen *et al.* 2003)	**Least-cost path**: A swath of landscape that is one pixel wide and represents the lowest cumulative cost between two patches (Verbeylen *et al.* 2003)	**Corridor**: A slice of landscape encompassing the most permeable percentiles of the cost surface **Habitat linkage**: Connective land that promotes movement/ dispersal for multiple species between core habitats (Beier *et al.* 2008; 2009)
Examples	Define source patches using: ▪ **Home Ranges** ➢ e.g. minimum convex polygon, kernel density estimator ▪ **Point Locations** ➢ e.g. direct observations, radio-telemetry, nest/den evidence ▪ **Habitat Suitability Analysis** ➢ e.g. Percentage of most suitable habitat ➢ Suitable habitat larger than a cut-off ▪ **Protected Areas** ▪ **Expert Opinion**	Decisions can be based on: ▪ **Expert Opinion Resource Selection Functions (RSF) or Habitat Suitability Index (HSI)** ➢ Derived from regression of occurrence data on environmental variables ▪ **Analyses of animal movement behavior** ➢ e.g., radio or satellite telemetry, snow tracking ▪ **Landscape genetic analyses** ➢ e.g., correlation of habitat elements with genetic differences	Resistance may signify: ▪ **Mortality risks** ▪ **Reproductive costs** ▪ **Energetic costs** ▪ **Physical resistance** ▪ **Thermal stress** ▪ **Habitat suitability**	Cost schemes can be determined using: ▪ **Expert Opinion** ➢ Analytical Hierarchical Process ➢ Mean response ➢ Qualitative ▪ **Species Habitat Preferences** ➢ Compositional analysis: time spent in each habitat type relative to availability ➢ RSF/HSI: Probabilistic map regressing presence on habitat variables ▪ **Analyses of animal movement behavior** ➢ Movement choice/speed in different habitat types & transitions ▪ **Gene Flow**: ➢ Correlation of gene flow estimates with effective dist. of cost scheme	The cost value in each cell represents effective distance to the source patch, measured in the least effort (lowest cost) of moving over the cost surface	The model creates the most likely travel route by selecting a combination of cells that represent the shortest effective distance between two designated patches (LaRue & Nielsen 2008)	Corridors can be identified by: ▪ **Buffer/Minimum Width**: ➢ Buffer LCP to chosen width (e.g. home range size) ▪ **Least Cost Corridor/ Probable Movement Zone**: ➢ Combine multiple low-cost routes ➢ Lowest percentile (10%, 20%, etc) of cost paths ▪ **Circuit Theory**: ➢ Delineate areas of landscape with highest "conductance" between patches ➢ Can incorporate patch characteristics ➢ Can be used to rank potential corridors, explore alternative corridors, and identify bottlenecks (McRae & Beier 2007)

Figure 2.

Legend: A comparison of four least-cost path models between two bighorn sheep populations in southern California highlights the sensitivity of results to model inputs. Cost surfaces used to produce the four paths incorporate the following landscape characteristics: topography alone (Optimized model); wooded habitat alone (Incomplete model); topography, habitat, and road density (Expert model); or topography, wooded habitat, and urban areas (Optimized Local model). Total least-cost path length overlapped less than 2%; least-cost corridors based on the lowest 10% of the resistance surface overlapped from 0 to 44%.



CHAPTER 5

Applying resource selection functions at multiple scales to prioritize habitat use by the endangered Cross River gorilla

ABSTRACT

Aim: The critically endangered Cross River gorilla is a patchily distributed taxon for which habitat selection has been modeled only at coarse spatial scales, using remotely-sensed landscape data and large-scale species distribution maps. These coarse-scale models fail to explain why Cross River gorillas (CRG) display a highly fragmented distribution within what appears to be a large, continuous area of suitable habitat. This study aimed to refine our understanding of CRG habitat use to inform conservation planning both for the subspecies and for other fragmented species of conservation concern.

Location: CRG occur only in a discontinuous distribution in the southern portion of the Cameroon-Nigeria border region, an area that represents one of Africa's biodiversity hotspots. This study was carried out in the Northern Mone-Mt. Oko region, part of the Mone/Mbulu forest system located in the Manyu division of the Southwest Province of Cameroon.

Methods: We used resource selection functions to understand habitat use by CRG at multiple scales. Specifically, we employed generalized additive models at the scale of the annual subpopulation range and conditional logistic regression at the scale of individual movements.

Results: CRG habitat selection is highly scale dependent. Localized measures of habitat quality strongly influenced selection at the subpopulation or landscape scale, while human activity and food availability were the best predictors of selection at finer scales.

Main conclusions: Understanding why CRG do not occur in seemingly suitable habitat is crucial for designating critical habitat both within and between CRG subpopulations. Our results indicate that conservation planning to maintain critical habitat and connectivity among CRG populations will require an integrative, multi-scale planning approach incorporating large-scale landscape characteristics, human use patterns and CRG food availability.

Keywords: conservation planning; critical habitat; Cross River gorilla; resource selection functions; spatial scale

INTRODUCTION

Habitat loss, degradation, and fragmentation are major drivers of recent biodiversity declines (Doerr *et al.,* 2011; Fahrig, 2003; Quinn & Harrison, 1988). In the face of land use and land cover changes, understanding the characteristics that influence species occurrence and persistence is critical to preventing biodiversity loss (Kopp *et al.,* 1998). Rapid assessments of species' habitat requirements, including both ecological and anthropogenic habitat influences, are necessary to inform land use and conservation decisions at multiple scales (Desbiez *et al*., 2009; Dussault *et al*., 2006; Labonne *et al*., 2003). Such assessments often rely on coarse-scale models due to the ease of access to remotely-sensed habitat information such as land cover data. While coarse-scale inferences are useful for landscape-level conservation planning, they are also likely to miss micro- and meso-scale ecological and anthropogenic elements critical to species habitat requirements, particularly for risk-sensitive and patchily distributed species (Howes & Lougheed, 2004; Sawyer *et al*., 2011). In many instances, land cover data alone will be inadequate to predict habitat constraints, and a combined approach that includes finer-scale analysis of ecological and anthropogenic factors influencing animal habitat selection is necessary for identification of habitat critical to the persistence of species of conservation concern (Bjorneraas *et al.,* 2011; Hirzel & Le Lay, 2008; Mayor *et al.,* 2009).

The Cross River gorilla (*Gorilla gorilla diehli*) is one such patchily-distributed species for which habitat characterization is essential to effective conservation. One of the world's most endangered and least studied primates, the Cross River gorilla occurs only in a discontinuous distribution in the southern portion of the Cameroon-Nigeria border region (Bergl & Vigilant, 2007; Bergl *et al.,* 2012; De Vere *et al.,* 2011). Cross River gorillas (hereafter: CRG) are estimated to have as few as 300 individuals remaining, divided into 14 fragmented subpopulations within seemingly intact habitat (Bergl *et al.,* 2012; Bergl *et al.,* 2008; De Vere *et al*., 2011; Sarmiento, 2003). To date, a lack of understanding of the relationship between CRG ecology and available habitat has hampered landscape conservation efforts. Available data has permitted only coarse-scale estimation of critical habitat for CRG persistence and connectivity based mainly on broad-scale, remotely-sensed data (Bergl *et al.,* 2012; Groves, 2002). These assessments indicate that the factors likely contributing to CRG habitat selection and suitability include: (a) habitat type, with preference for highland over lowland forest, and (b) human utilization, particularly hunting, with CRG preferring steeper, higher elevation areas that are farther from villages and harder for humans to access (Bergl *et al.,* 2012; Groves, 2002; McFarland, 2007). Such macro-scale habitat selection models provide an important first step for predicting CRG distribution, but they must be refined by considering the determinants of suitability and connectivity at scales relevant to movement decisions by individuals (Doerr *et al*., 2011).

Resource Selection Functions (RSFs) represent an important tool to understand species habitat requirements at multiple scales and provide theoretical foundations for applied habitat management decisions (Hirzel *et al.*, 2006; Howes & Lougheed, 2004; Kopp *et al.,* 1998). An RSF is a statistical model that indicates the probability of use of a particular resource type by a given individual or group, and is used to identify non-random species-habitat associations (Boyce, 2006; Boyce & McDonald, 1999; Kirk & Zielinski, 2009; Labonne *et al.*, 2003). Resources can include a broad range of ecological and anthropogenic characteristics, species interactions, and food items, and selection is derived by comparing levels of use to availability for each resource (Buskirk & Millspaugh, 2006). RSFs allow managers to model current and future species distributions, predict the potential impacts of ecosystem degradation and management actions on habitat use, and conserve essential resources for endangered species (Martinez-Meyer *et al.*, 2006; Millspaugh *et al.*, 2006). RSFs may be particularly valuable in conservation decision-making for patchily-distributed species, and can complement more macro-scale species distribution models by identifying critical habitat both within and between fragmented populations (Harris *et al.*, 2008).

The influence of particular landscape characteristics on species' habitat use and movement within and between subpopulation patches will vary with scale, and both resource selection decisions and conservation/management actions are thus highly scale-dependent (Gustine *et al.,* 2006). RSF models can be applied at multiple scales in a hierarchical approach to understand the influence of scale and link macro-scale distribution models to decision-making by individual animals (Mayor *et al.*, 2009). Because RSF models can consider habitat selection by individuals, groups, populations, and taxa, they can provide an important tool to incorporate scale into both ecological understanding and conservation decision making, particularly for fragmented, risk-averse species (Meyer & Thuiller, 2006).

Johnson (1980) describes four orders of resource selection by species from coarse to finer spatial scales: (1) choice of the geographic range by a taxon; (2) choice of a use area (e.g., home or subpopulation range) within the geographic range; (3) use of a habitat component or area (e.g., forest patch) within the home range; and (4) selection of a specific resource (e.g., nest site, food source, etc.) within a selected area (Buskirk & Millspaugh, 2006; Johnson, 1980). These four levels may provide very different perspectives on species resource selection, each one important for management decisions. Rarely, however, do studies incorporate and communicate across scales. To date, only the first order of selection has been examined for the Cross River gorilla, due mainly to a lack of data at finer scales (*Bergl et al., 2012*). We used a multi-scale approach to assess resource selection at progressively finer scales by one CRG subpopulation living in the Mone Forest Reserve in Cameroon. Our three levels of analysis include: (1) coarse-scale selection of subpopulation range compared to available resources in the study area; (2) intermediate-scale selection of resources compared to available resources within the current subpopulation range; and (3) fine-scale selection of resources by a gorilla group compared to resources available within an average day's journey length of selected locales (Boyce, 2006; Ciarneillo *et al.*, 2007; McLoughlin *et al.*, 2004; Perkins & Conner, 2004). By integrating resource-selection across spatial scales, this study helps to define critical CRG habitat for both persistence within and connectivity among CRG subpopulations. It also endeavors to illustrate the utility of applying a hierarchical habitat selection framework to inform decision-making in conservation.

METHODS

Study Site and Data Collection

Surveys to assess Cross River gorillas' (CRG) habitat use were conducted in the Northern Mone/Mount Oko region. This region is part of the Mone/Mbulu forest system located in the Manyu division of the Southwest Province of Cameroon and represents one of Africa's biodiversity hotspots (Asaha & Fru, 2005; Forboseh *et al.,* 2007; Nku, 2004; Fig 1). The Mone-Mbulu area has an estimated human population of approximately 6,300 individuals, living within 30 widely dispersed villages (Asaha & Fru, 2005). Households in the area are mainly dependent on subsistence hunting and agriculture, but income is also generated through the sale of various forest and farm products, teaching, construction, and remittances from urban-living relatives (Asaha & Fru 2005). Access to markets, health facilities, and education is limited in the region; and infrastructure, for both transportation and communication, is generally lacking (Asaha & Fru 2005).

The Northern Mone/Mount Oko region includes the northern portion of the 560 km^2 Mone River Forest Reserve, designated as a production forest by the national government, and the Southern portion of the Mbulu forest, called Mt. Oko (Fig 1a). Despite its status as state-run, the Mone Reserve remains under the *de-facto* control of local communities, who are largely unaware of the forest's ownership status and associated forestry laws (Asaha & Fru 2005). The general pattern of land cover in the area consists of farmland which extends up to a few kilometers (kms) from villages, progressing to secondary forest and fallow farmlands farther from villages, transitioning to forested areas ranging from 100 to 1500 m in elevation. The region experiences two distinct seasons, with most of its up to 4500 mm yearly rainfall occurring between April and November, and with average annual temperatures around 27º C (Groves 2002).

The Mone/Mount Oko region contains at least one of the fourteen known subpopulations of CRG. Very little data on potential CRG locations within the region were available prior to this study, and little was known about if and how CRG utilize this portion of the landscape. Because the potential CRG habitat in the area is quite large, we calculated a minimum convex polygon (MCP) of known gorilla sighting or sign locations (N = 38) over the previous 10 years in the Mone-Mt. Oko region was calculated in ArcGIS (ESRI 2011) to guide delineation of the survey area (Fig. 1a). These location data were collected and generously shared by the Wildlife Conservation Society's Takamanda Mone Landscape Project. Due to the limited amount of data, the limited knowledge as to how many subpopulations potentially existed in this area, and the limitations of MCP in detecting non-utilized areas within the polygon, the calculated

MCP was not intended to approximate the actual CRG subpopulation range but rather to facilitate targeted surveys. Only 6 data points, some already very old at the time of observation, were available for from the Mt. Oko area, and visual assessments suggest that these points may belong to the southern-most forays of a more Northern subupopulation, as they are disjunct from CRG fixes within the Mone Reserve (Fig 1a). From November 2009 through August 2010, we conducted guided reconnaissance and travel surveys in and adjacent to the MCP to search for gorilla sign, and to measure CRG vegetative food species availability and habitat characteristics in sampling plots at 500 meter intervals (Kuhl *et al.,* 2008; McNeilage *et al.,* 2006; Sawyer, 2012; Fig 1b). Guided reconnaissance surveys follow the path of least resistance while deviating no more than 40° from a set compass bearing (Kuhl *et al.,* 2008), and were placed no more than 500 m apart to avoid missing CRG use of a particular area (McNeilage *et al.*, 2006). The placement of reconnaissance survey's no more than 500-700 m apart minimizes the chance that gorilla use of any area went undetected (McNeilage *et al.*, 2006). When we found recent gorilla sign, we abandoned the compass bearing and followed the CRG feeding path (i.e. travel survey). A total of 262 km of surveys were walked in this manner (Fig 1b). No CRG sign was observed in the Mt. Oko area during this study (Fig 1b).

This study relied on indirect sampling methods due to the risks to CRG safety associated with their habituation (Doran *et al.,* 2002; Rogers *et al.,* 2004; Sunderland-Groves *et al.,* 2009). As hunting pressures in the area are high, and law enforcement levels quite low, habituating CRG to human presence may significantly increase their risk to hunting and disease transmission by humans. Additionally, the difficult terrain and large study area would make following even habituated CRG quite challenging. Specifically, we recorded nest sites, trampled vegetation, dung, and feeding sign (chewed, broken, and discarded vegetation), and estimated the approximate date of use by the CRG for each sign. Nest sites are easily identified areas where all weaned individuals in gorilla groups make nests in close proximity to one another, and this cluster changes location each night (Ganas *et al.,* 2008; Schaller, 1963; Williamson, 1988). During the day, gorillas move between nest sites, leaving characteristic remains of their feeding and movement (Rogers *et al.,* 2004). Gorillas trample vegetation, discard the least nutritious portions of their food plants, and defecate frequently, resulting in an easily identifiable "feeding trail" (Ganas *et al.,* 2008; Rogers *et al.,* 2004). Nest sites and foraging signs remain intact and easily identifiable for many months (170 – 189 days; Williamson & Usongo 1996; Brugiere & Sakom, 2001) and visible for even longer, and can be aged to reflect approximate date of gorilla habitat use within the past year (Brugiere & Sakom, 2001; McFarland 2007). Age of gorilla sign in this study was estimated by local expert hunters/trackers to within ±1 month using their knowledge of plant decomposition rates in the area (Sawyer 2012). Because confusion can occur between chimpanzee and gorilla nests in this landscape, trackers tried to use secondary indicators such as footprints, dung, feeding sign, or vocalizations to ensure nest sites were correctly attributed to CRG. We took a conservative approach to nest identification, including in the analysis only nests where all hunters/trackers agreed with near or complete certainty of CRG origin. However, some signs may have been miss-attributed to CRG or chimpanzee, which may have affected our results. We discuss the implications of these potential errors in our discussion.

In addition to recording gorilla sign, we carried out visual habitat assessments within 477 ten-meter-diameter circular vegetation plots, placed at 500 m intervals along both guided and travel reconnaissance trails. Within sampling plots we recorded the following habitat characteristics: habitat type, canopy cover, undergrowth thickness, dominant undergrowth type, slope, presence or absence of signs of human use, and presence or absence of signs of gorilla use. Human sign recorded included: cartridges, traps, machete marks, trail demarcation, foot prints, huts/sheds, and any other clear sign of forest product use. We also enumerated stem counts of vegetative (herbaceous/fibrous) CRG food species and presence/absence of seven important non-timber forest products within sampling plots (unpublished data; Table 1). Important fibrous (vegetative) species were defined as those consumed on greater than 5% of the observed feeding trail days (Doran et al., 2002; Ganas et al., 2004; Sawyer unpublished data). Logistical constraints prevented us from including fruit species, an important part of the CRG diet, in the analysis. Additional research will be necessary to monitor fruit species in the landscape, and will provide essential information to improve upon out analyses. We recorded location coordinates for all CRG signs, sampling plots, human signs, and other wildlife signs using a Garmin GPS and Cybertracker.

Data Analysis

We developed resource selection models for three levels of spatial analysis using the survey data collected over the 10-month study period (Buskirk & Millspaugh; 2006; McLoughlin *et al.,* 2004; Perkins & Connor 2004). To do this, we started by estimating the CRG subpopulation range using the Local Convex Hull modeling technique (Calenge, 2006; Getz *et al.,* 2007; Sawyer 2012; Fig 1c). To minimize issues associated with spatial autocorrelation without removing the biological signals of interest, we used all gorilla nest-sites from this study and only one feeding sign per day, for a maximum of 2 location points for each day of gorilla use (De Solla *et al.* 1999; Fieberg 2007; Hayward *et al.* 2009; Swihart & Slade 1985). As sign remained visible for many months after use, we estimate that the data represented approximately 20 months of gorilla use (Sawyer 2012). Western gorilla ranges are fairly stable through time (compared to mountain gorillas which exhibit interannual home range overlap of 50-73%; Doran-Sheehy *et al. 2004* ; Bermejo, 2004; Robins & McNeilage, 2003) and CRG likely used at least 80% of their subpopulation range over the 20 months represented in our data sample (Bermejo, 2004). The subpopulation range size reached an asymptote in this analysis, allowing approximate estimation of current subpopulation ranging patterns with the data collected over 10 months (Doran-Sheehy *et al.*, 2004; Sawyer, 2012).

We assessed resource selection by CRG at the scale of the subpopulation range by comparing habitat characteristics within the CRG subpopulation range to those available within the study area (Ciarneillo *et al.*, 2007; Dussault *et al.*, 2006; McLoughlin *et al.,* 2004). Our second level of analysis compared habitat characteristics of areas where we found sign of gorilla use to overall availability of those habitat features within the current subpopulation range (Johnson, 1980). Our third level of analysis examined the day-to-day habitat selection by individuals. Specifically, we paired used and neighboring unused locations on a local scale to evaluate fine-scale patterns of habitat selection (Buskirk & Millspaugh, 2006; Godbout & Ouellet, 2010). For this third level of analysis, each location where gorilla use was confirmed was paired with five randomly selected available locations within a buffer distance deemed to be the average distance a Cross River gorilla can travel within a day (Boyce, 2006; Buskirk & Millspaugh, 2006; Ciarniello *et al.*, 2007; Compton *et al.*, 2002; Cooper & Millspaugh, 1999). This distance was conservatively set at 1.5 km based on observed daily travel distances of the ecologically-similar eastern lowland gorilla (unpublished data; Yamagiwa *et al.,* 1994).

For the first two levels of analysis, we developed a generalized additive model (GAM) to create the resource selection function. This approach creates a probability of gorilla resource use in relation to habitat, food, and human use variables using a logit link function with the gamlss command in R statistical package (Panigada *et al.*, 2008; R Development Core Team, 2010). Modeled variables are listed in Table 1. We used GAMs because initial exploration of scatterplots from locally-weighted polynomial regressions revealed non-linear relationships among parameters, and GAMs are more flexible in incorporating non-linear relationships than generalized linear models (Boyce, 2006; Hirzel & Le Lay, 2008; Panigada *et al.,* 2008). GAMs were fit using a reverse stepwise procedure with the stepGAIC function in R statistical package for a set of candidate variables including all habitat and human use measures, and the most frequently observed vegetative food species in the CRG diet (Carroll *et al.,* 1999; Kirk & Zielinski, 2009; Sawyer unpublished data). The third level of resource selection analysis employed a conditional logistic regression approach, using the clogit command in the survival package in R to compare CRG used sites with available resources in a 1.5 km buffer zone (Cockle *et al.*, 2011; Compton *et al.*, 2002; Duchesne *et al.,* 2010; Therneau 2012).

For all three spatial scales of modeling, we tested for collinearity of candidate variables using variance/covariance matrices, and variables with a correlation coefficient (*r*) greater than 0.7 were not included together in the models (Ciarniello *et al.*, 2007; R Development Core Team, 2010). Where collinearity occurred, we retained the most easily measured habitat variable (e.g. elevation or slope rather than food stem densities). For predictor variables exhibiting correlation coefficient values between 0.6 and 0.7, we retained only the residuals of a linear regression of the more complex against the simpler habitat measure to identify any remaining effect of the complex habitat measure unexplained by variables already in the model. We used AIC values to select relevant variables (Burnham & Anderson, 1998; Harris *et al.*, 2008; Horne *et al.*, 2008; Kirk & Zielinski, 2009; Zielinski *et al.*, 2004), and we considered models comparable if the delta AIC was less than 2.0 (Ciarniello *et al.*, 2007). For models with similar AIC values, we chose the model with fewer terms (Quinn & Keough, 2002). To minimize the effect of spatial autocorrelation in the data, we included UTM coordinates as covariates in the model (Boyce, 2006; Boyce & McDonald, 1999; Carroll *et al.*, 1999).

Additionally, we included GPS point density as a measure of search effort because travel reconnaissance surveys can lead to high concentration of search effort in areas where gorilla sign is found (Panigada *et al.*, 2008; Table 1).

RESULTS

Annual Subpopulation Range Selection

Resource selection by Cross River gorillas (CRG) exhibited strong, non-linear relationships with elevation, slope, and distance to nearest village at all scales of analysis (Figs 2 & 3). At the coarsest scale of analysis, variables retained in the final model predicting selection of the current CRG subpopulation range were generally localized measures of habitat quality (Table 2). Though neither remotely-sensed habitat type nor ground-truthed habitat type had predictive power at the scale of subpopulation range selection, more localized habitat quality characteristics were significant in the model. CRG showed preference for areas with more open canopy and understory, characteristic of light gaps which may promote herb growth (White *et al.*, 1995). In addition, slope remained important in the model, and CRG selected their range within areas of 10-25% slope, indicating avoidance of both flat and very steep areas (Fig 2, Table 2). Altitude was also significant, but contrary to findings of previous studies (Bergl et al., 2012; Groves 2002; Oates *et al.,* 2003), our best model suggested CRG selected mid-elevation areas over both low and high elevations (Fig 2, Table 2). While the study site averaged 740 masl (range 56 – 1744 masl), the average gorilla sign was observed at 504 masl (range 75 – 1207 masl). Additionally, 77% of gorilla signs observed were found below 650 masl. This likely represents an underestimation of lowland use, as GPS altitude readings were much more difficult in lowland sites, and we were often unable to record elevation at these sites. Finally, most measures of human use (i.e., human sign, distance to human sign) were not retained in the best model, and distance to the nearest village was retained but was not significant (Fig 3, Table 2), indicating a low importance of human resource use in subpopulation range selection.

Habitat Use Within the Subpopulation Range

Within the current CRG subpopulation range, food availability and human utilization were significant predictors of habitat selection, in addition to localized habitat quality indicators (Table 2). Similar to our macro-scale analysis, canopy openness and elevation were significant predictors of CRG habitat selection within the subpopulation range, but undergrowth thickness and slope were not significant at this finer scale. In addition, the two most commonly consumed herbaceous food species remained in the best model, with CRG selecting habitat with higher stem densities of these foods (unpublished data; Table 2, Figure 4a). Measures of human use were negatively correlated with CRG habitat use within the subpopulation range, indicating avoidance by CRG of heavily exploited areas (Table 2, Fig 4b). The majority of human sign encountered (873 of 893 signs) was either directly related to hunting (ie cartridges, snares; n = 404) or indirectly related (ie hunting trails and bush huts; n = 469). Thus, human sign in this study should be considered a proxy for hunting pressure, while NTFP presence should provide a proxy for other harvesting actions. However, even with search effort accounted for in the model, areas nearer to villages were slightly preferred to farther ones within the range (Fig 3). Finally, presence of forest products (NTFPs) important for human use was also negatively correlated with gorilla habitat selection, though no spatial relationship was detected between the distribution of these forest products and the abundance of preferred CRG food species (Table 2).

Habitat Use Within Daily Travel Distance

At the finest scale of habitat selection – within an average day journey length from CRG sign - availability of monitored staple food species was a primary predictor of CRG habitat selection. The availability of the four most commonly eaten herbaceous species, *Cercestis cameronensis*, *Stylochaeton zenkeri*, *Aframomum* sp, and *Palisota* sp, was positively correlated with CRG habitat selection (Table 2). As in the coarser models, measures of human impact (both hunting and other harvest activities) were significant at the finest scale, with human use and proximity to human use negatively affecting CRG habitat selection (Table 2). Measures of local habitat quality were also significant predictors of CRG selection, with selection towards more open, mid-elevation areas, and against those areas dominated by liana understory and with high availability of human-exploited NTFPs (Table 2).

DISCUSSION

This study developed resource selection functions to identify factors critical to the distribution of the Cross River gorilla at multiple spatial scales. In so doing, it begins to shed more light on the forces driving the current distribution of Cross River gorillas (CRG) and confirms that resource selection by CRG, like that of many wide-ranging species, is highly scale specific (Baasch *et al.*, 2010; Boyce, 2006; Dussault *et al.*, 2006; McLoughlin *et al.*, 2004). While our data collection was limited my many factors, and our results should be interpreted with caution, we hope that this initial glimpse into resource selection by CRG will both inform conservation measures but also encourage further research to flesh out our findings.

To date, the factors limiting the fragmented distribution of CRG have not been well understood, as coarse-scale models indicate high levels of suitable but unoccupied forest in the region (Bergl *et al.*, 2012; Bergl *et al.*, 2008; Oates *et al.*, 2003). Genetic evidence suggests that CRG have recently experienced a population bottleneck. While underlying causes for extirpation from previously inhabited sites remain largely unknown, hunting may have been a major contributor to general population declines (Bergl *et al.*, 2008; Bergl *et al.,* 2012; Thalmann *et al.* 2011). This study indicates that while remotely-sensed habitat characteristics like slope and elevation may be useful predictors of CRG distribution at the coarse scale, human activities and food availability become more important to finer scale selection, where CRG likely make day-to-day movement decisions. These findings highlight the utility of hierarchical resource selection functions (RSFs) to better understand resource use by focal species. However, this study was only able to include areas occupied by one of the 14 subpopulations, and areas directly surrounding this subpopulation range. Thus, results should be interpreted conservatively and, as similar data become available for areas within and surrounding additional subpopulations, more robust conclusions will evolve.

Subpopulation range selection by CRG preferentially included areas with partially open canopy and undergrowth cover. This may indicate a preference for highly herbaceous areas (White *et al.*, 1995), as terrestrial herbaceous vegetation is a keystone resource for gorillas and can serve as an important buffer during periods of low fruit availability (Brugiere & Sakom, 2001; Yamagiwa *et al.* 1994; Yamagiwa *et al.,* 2005). Selection at the subpopulation range scale also showed preference for areas at mid-elevation levels with low- to mid- slope. These results represent a divergence from more coarse-scale studies, which highlight steep slope, highland forest areas as highly suitable for the CRG (Bergl *et al.,* 2012; Groves, 2002; Sunderland-Groves, 2008). Thirty percent of observed gorilla sign occurred below 400 masl and half occurred within flat or gently sloping areas. An explanation for the observed differences of this study to previous findings may be the failure of macro-scale analyses to incorporate trade-offs between resource abundance and potential risks on the landscape (Fig 4). Resource selection often requires trade-offs between food availability and exposure to potentially detrimental factors (Bastille-Rousseau *et al*., 2010; Dussault *et al.,* 2006). Furthermore, understanding food availability in this system requires more fine-scale data than coarse habitat type alone. Our observation of selection by CRG of mid-elevation and intermediate slopes at the subpopulation range scale may thus represent a compromise between attraction to staple food species (higher at lower elevations) and avoidance of human activity, particularly hunting (also higher at lower elevations) (Fig 5). To date, food distribution has often been overshadowed by hunting impacts in our understanding of CRG ranging patterns. This study highlights the importance of both factors, and their potential interaction, in determining current CRG distribution. We were unable, due to logistical constraints, include important fruit food species in our analysis, and these species will undoubtedly exert significant forces on CRG ranging. Future studies should incorporate phenology and dietary analysis to better understand both fruit in the CRG diet, as well as its spatial and temporal distributions in the landscape.

Though human activity seemed to have little influence on CRG habitat use at the scale of subpopulation range selection, likely an indication that human use is fairly uniform and unavoidable at the largest scales within the landscape, new patterns of resource selection emerge within this range. CRG select areas of lower human use within their subpopulation range and at the scale of daily journey-distances (Fig 4b). While human activities in the region include collection of many non-timber forest products (NTFPs), hunting activities appear to be the strongest determinate of CRG habitat use. Most signs of humans we recorded were hunting related. Like many wildlife species, CRG are threatened by hunting, which operates both directly on species' abundance by removing individuals, and possibly indirectly by raising stress levels, changing behavior, and reducing reproductive output (Bergl *et al.*, 2012; Pauli & Buskirk, 2007; Robinson *et al.,* 1999; Wilkie & Carpenter 1999). Wildlife harvest studies in the region indicate that one to three CRG are harvested annually, though this is likely an underestimate (Oates *et al.*, 2003; Sawyer & Sawyer, 2011). While hunting gorillas is illegal in Cameroon, law enforcement in the region has been largely absent or ineffective (Bergl *et al.*, 2012; Oates *et al.*, 2007; Sawyer & Sawyer, 2011). Additionally, though most local hunting does not target gorillas, hunting of other species is common in the area (Mboh & Warren, 2007), which may indirectly affect CRG through stress and behavioral responses, resulting in avoidance of areas associated with human utilization and leading to decreased connectivity among subpopulations.

In addition to human impacts, availability of staple food species influenced CRG habitat selection within the subpopulation range. The two most common herbaceous/vegetative species in CRG diet were shown to influence habitat use on a broader scale, while at a finer scale, where individual movement decisions are made, all four of the staple herbaceous food species influenced habitat use (Sawyer unpublished data). Food is an important limiting factor to species' abundance and distribution, and many primate populations have been observed to decline significantly when key food species are selectively removed through logging or other processes (Chapman *et al.*, 2006). Recent studies examining gorilla distributions indicate that western gorillas occur at higher densities in areas where their staple foods are most abundant (Rogers *et al.*, 2004), and that food availability has important implications for population dynamics, including carrying capacity (Nkurunungi *et al.*, 2004). The distribution and relative abundance of resources likely influences many aspects of gorilla sociality and ranging patterns (Doran-Sheehy *et al.*, 2004), particularly when they are dependent on rich, dense food species distributed patchily in time or space. Food availability has largely been ignored in landscape-scale connectivity and conservation modeling for CRG due to a lack of data. However, this study indicates that coarse-filter habitat type may have little correlation with food availability on the landscape, and may therefore act as a poor proxy for habitat suitability for the CRG. Our results suggest that understanding food availability across the landscape will be essential for identifying critical CRG habitat, and further studies will be needed to examine availability across the region, and include non-herbaceous food items like fruit and bark.

An important limitation of this study is the incomplete food species we were able to include in our analysis. While seasonal species, particularly fruit, are important to the CRG diet, we were unable to gather information on these species. Thus, while our results suggest the importance of food in CRG habitat use, we are likely underestimating this importance, and we are unable to detect patterns of how this importance may change across seasons. Thus, our results should be interpreted cautiously, and additional studies over multiple seasons over multiple years will aid researchers in detecting the levels of importance of various food species in CRG ranging patterns to make better conservation decisions.

Another limitation of this study, and most others that apply resource selection functions, is that it assumes that species occur most frequently in the most suitable habitat (Dussault *et al.*, 2006; Hirzel & Le Lay, 2008). It would be more realistic, though substantially more challenging for long-lived species like the CRG, to use fitness measures rather than presence/absence to quantify the importance of habitat selection for population persistence (Dussault *et al.*, 2006). In addition, detection error will affect reliability of resource selection functions (Boyce, 2006), and expanding data collection over a longer time period, testing detection error rates, and using more direct measures of gorilla presence could further improve study methods. Model validation is a key component for assessing the utility of RSFs (Coe *et al.*, 2011; Hirzel *et al.*, 2006; Howes & Lougheed, 2004; Johnson & Gillingham, 2008; Wiens *et al.*, 2008). Challenging field conditions led to small sample sizes in our study and we were unable to independently validate the resulting RSFs. Further data collection in the region will be valuable for model validation.

Another important limitation of this study was the potential for misidenfication of CRG nests, due to the difficulty in differentiating gorilla nests from chimpanzee nests in the region. This may have led to both the inclusion of chimpanzee nests unwittingly into the analysis, as well as exclusion of CRG nests if trackers could not agree on the nest source. Exclusion of CRG nests thought by our team to be chimpanzee nests might have led to the exaggeration of the predictive ability of the variables retained in our models. Inclusion of chimpanzee nests in the analysis may have masked the predictive power of habitat traits. A study of resource selection by chimpanzees in an area of the region where (a) the potential habitat area is smaller; and/or (b) gorillas are at least partially habituated to human presence might help researchers to better detect these potential conflations. In the meantime, our conclusions should be applied cautiously and further data collection should be encouraged.

Logistical constraints, including time, funding, safety of field workers, and the difficulty of the terrain, limited the temporal and spatial scope of this study. Very little is known about the niche ecology of this critically endangered subspecies, and we hope that the limitations of this study will encourage others to pursue further research in the area. Data collection on a larger spatial scale, and extended over multiple years will greatly improve the model utility to predict suitable CRG habitat into the future.

CONCLUSIONS AND FUTURE DIRECTIONS

This study highlights the utility of integration across multiple scales of resource selection to inform management strategies. A different picture of critical CRG habitat is presented with each progressively finer scale of resource selection, and together these scales produce a more complete understanding of relationships between species distribution and behavior. When conservation planning relies on coarse-scale habitat models, it is essential that included variables do not mask finer scale habitat selection decisions and trade-offs (Sawyer *et al.*, 2011, Beier *et al.*, 2008). Predictor variables that have direct ecological significance are always preferable to surrogate variables, such as habitat type and distance to nearest village, which have only indirect association to causal factors but are often the only available data (Kirk & Zielinski, 2009). Our study suggests that both habitat type and distance from villages may be poor proxies for the landscape variables influencing Cross River gorillas (CRG) habitat use. Instead, conservation planning to ensure persistence of CRG subpopulations requires a closer look at staple food availability and human activities, both hunting and other NTFP harvest, throughout the landscape to determine what proportion of remaining forest represents unsuitable versus unoccupied habitat and to inform protection of critical habitat areas (Bergl *et al.*, 2012). The subtleties of sustainable and compatible human landscape uses are unclear and must be explored further. This study is limited in scope, and while a large-scale, data-intensive study may be expensive and logistically difficult, it will prove critical for gaining a deeper understanding of CRG niche ecology while informing habitat conservation planning in the face of land-use and land-cover change in the region.

Tables:

Table 1: Variables included in resource selection models for the Cross River gorilla (CRG).

Variable	**Description**
CRG Sign*	Presence or absence of sign of CRG use within last year
Altitude	Elevation of plot (GPS measurement)
Search Effort	density of GPS tracklog points within a one kilometer radius – indicator of time spent within one kilometer of plot, generally longer on travel than reconnaissance surveys due to indirectness of CRG routes
Distance to Village	Distance in kilometers to the nearest village
Distance to Human Sign	Distance to the nearest sampling plot where human sign was recorded
Slope	Categorical measure of steepness of slope, on a scale of 0-3
Habitat Type	Categorical measure of habitat type: Montane forest, Ridge forest, Lowland forest, disturbed/secondary forest, bare soil
Canopy Closure	Categorical measure of percent canopy cover at center of vegetation plot, scaled from 1-4
Understory Thickness	Categorical measure of undergrowth density throughout plot, scaled from 1-4
Understory Type	Dominant understory vegetation type: Herbs, Bushes, Lianas, Shrubs, Rocky/Open, Grass
Human Sign	Measure of human impact, from 0-4 where 0: no human sign, 1: human sign visible from but not within plot, 2: plot on human path or including harvest sign, 3: past farming, clearing, or burning evident, 4: current farm or village land. Human signs included: cartridges, traps, cutting sign, trail demarcation, foot prints, hut/shed, use of forest products (e.g. honey extraction)
Individual Food Species	Stem counts of important food species: *Cercestis camerunensis*, *Stylochaeton zenkeri*, *Palisota spp*, *Aframomum spp*, and 4 additional herbaceous spp were tested
Total NTFPs	Number of seven of the main Non-Timber Forest Products present in the plot. NTFPs identified as present or absent included: Palm spp, Cola spp, Spices, Cattle Stick, Bush Mango, Country Onion, Bush Pepper, and Fish Poison
Remotely Sensed Habitat Type	Habitat type classified using Landsat Imagery: Primary Forest, Secondary Forest/Agriculture, Water, Rock/Bare Soil

* Dependent Variable

Table 2. Predictor variables retained in the best resource selection functions for Cross River gorillas at three spatial scales of selection

Selection Scale	**Subpopulation Range**		**Within Subpopulation Range**		**Within Day Journey Distance**	
Covariate*	Coefficient	P	Coefficient	P	Coefficient	P
Habitat Type	-	-	-	-	-	-
Altitude	**-0.002**	0.000	**-0.003**	0.020	**-0.004**	0.000
Slope	**0.342**	0.042	-	-	-	-
Canopy Closure	**-1.554**	0.000	**-1.892**	0.000	**-1.860**	0.000
Undergrowth Thickness	**-0.423**	0.010	-	-	0.272	0.059
Liana Understory	-	-	-	-	**-0.808**	0.002
Distance to Village	-0.0003	0.079	-0.0002	0.497	-	-
Human Sign	-	-	**-0.866**	0.000	**-1.104**	0.000
Distance to Human Sign	-	-	**0.006**	0.043	**0.003**	0.025
Total NTFPs present	-	-	**-0.414**	0.001	**-0.225**	0.004
Cercestis camerunensis	-	-	**0.053**	0.014	**0.025**	0.044
Stylochaeton zenkeri	-	-	0.014	0.052	**0.018**	0.000
Aframomum spp	-	-	-	-	0.070	0.051
Palisota spp	-	-	-	-	0.034	0.065

* Spatial Coordinates and Search Effort retained in all models

Table 3. Model description and AICc values for a representative subset of tested models.

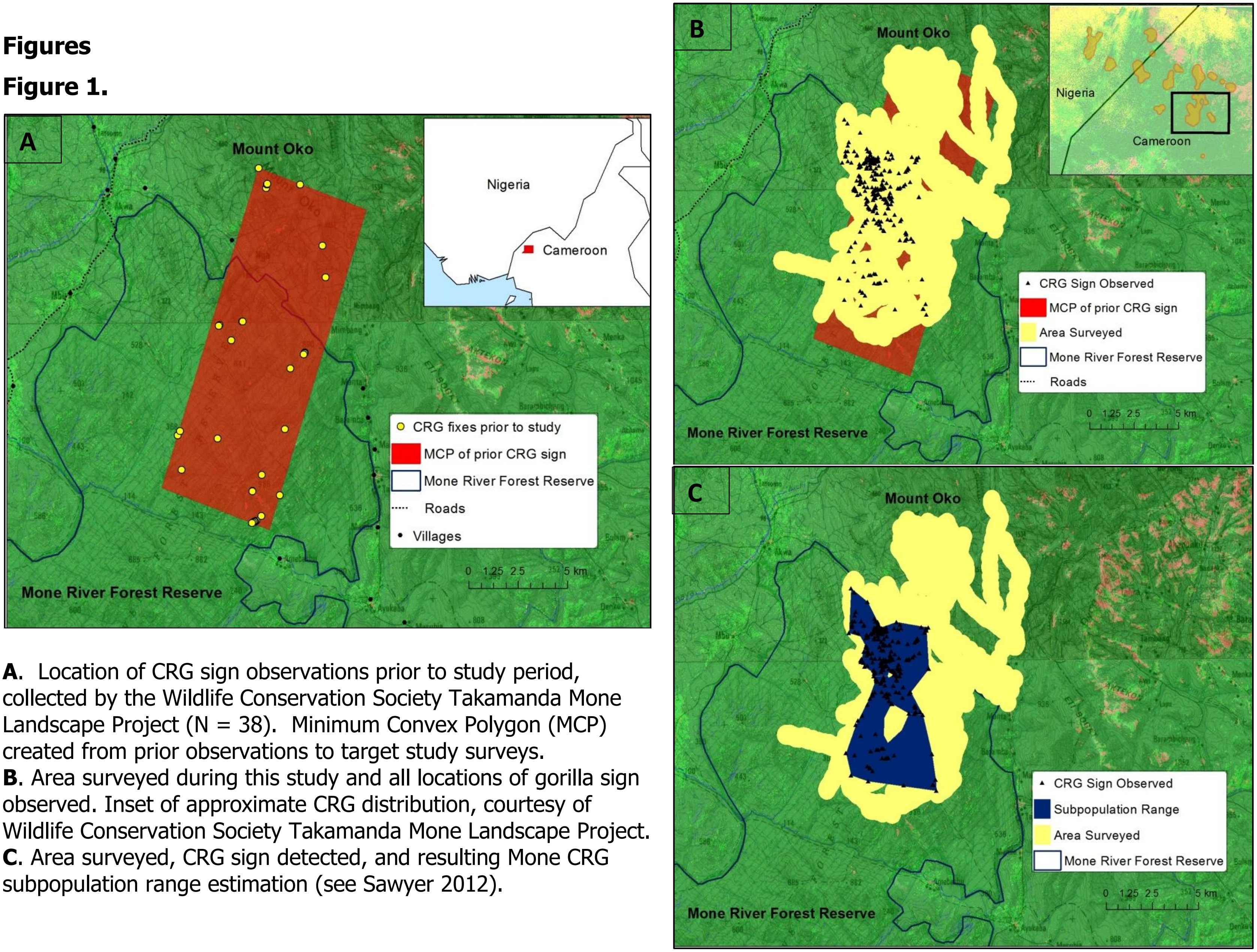
Model Name	Parameters Included	AICc Sub-population range	ΔAICc	AICc Within Sub-population range	ΔAICc	AICc within Day Journey	ΔAICc
Best Model	**See table 2 for parameters**	**323.13**	**0**	**207.41**	**0**	**335.39**	**0**
*Full Model**	All parameters in Table 1	338.26	15.13	226.95	19.54	*340.27*	*4.88*
Topography	Slope + Altitude	385.05	61.92	319.22	111.81	671.75	336.36
Preferred Foods	*Cercestis camerunensis* + *Stylochaeton zenkeri*	406.14	83.01	318.83	111.42	682.3	346.91
Human Use	Distance to village + Distance to human sign+ human sign + NTFPs	402.03	78.9	261.75	54.34	530.57	195.18
Remote Habitat	Remote Habitat Type + Distance to Village + Slope + Altitude	379.04	55.91	323.33	115.92	655.73	320.34
*Local Habitat**	Slope + Altitude + Understory Thickness + Canopy Closure	*325.98*	*2.85*	249.53	42.12	442.05	106.66
Habitat & Food	Slope + Altitude + Understory Thickness + Canopy Closure + *Cercestis camerunensis* + *Stylochaeton zenkeri* + *Aframomum spp* + *Palisota spp*	328.08	4.95	246.5	39.09	405.81	70.42
Habitat & Humans	Slope + Altitude + Understory Thickness + Canopy Closure + Distance to village + Distance to human sign + Human sign + NTFPs present	328.36	5.23	220.82	13.41	368.65	33.26
*Habitat, Food, & Humans**	Slope + Altitude + Understory Thickness + Canopy Closure + Distance to village + Distance to human sign + Human sign + NTFPs present + *Cercestis camerunensis* + *Stylochaeton zenkeri* + *Aframomum spp* + *Palisota spp*	330.43	7.3	*217.83*	*10.42*	346.62	11.23

Best Model shown in bold

***** Model with the second most support from the data at each scale is shown in italics

Figures

Figure 1.



A. Location of CRG sign observations prior to study period, collected by the Wildlife Conservation Society Takamanda Mone Landscape Project (N = 38). Minimum Convex Polygon (MCP) created from prior observations to target study surveys.
B. Area surveyed during this study and all locations of gorilla sign observed. Inset of approximate CRG distribution, courtesy of Wildlife Conservation Society Takamanda Mone Landscape Project.
C. Area surveyed, CRG sign detected, and resulting Mone CRG subpopulation range estimation (see Sawyer 2012).

Figure 2

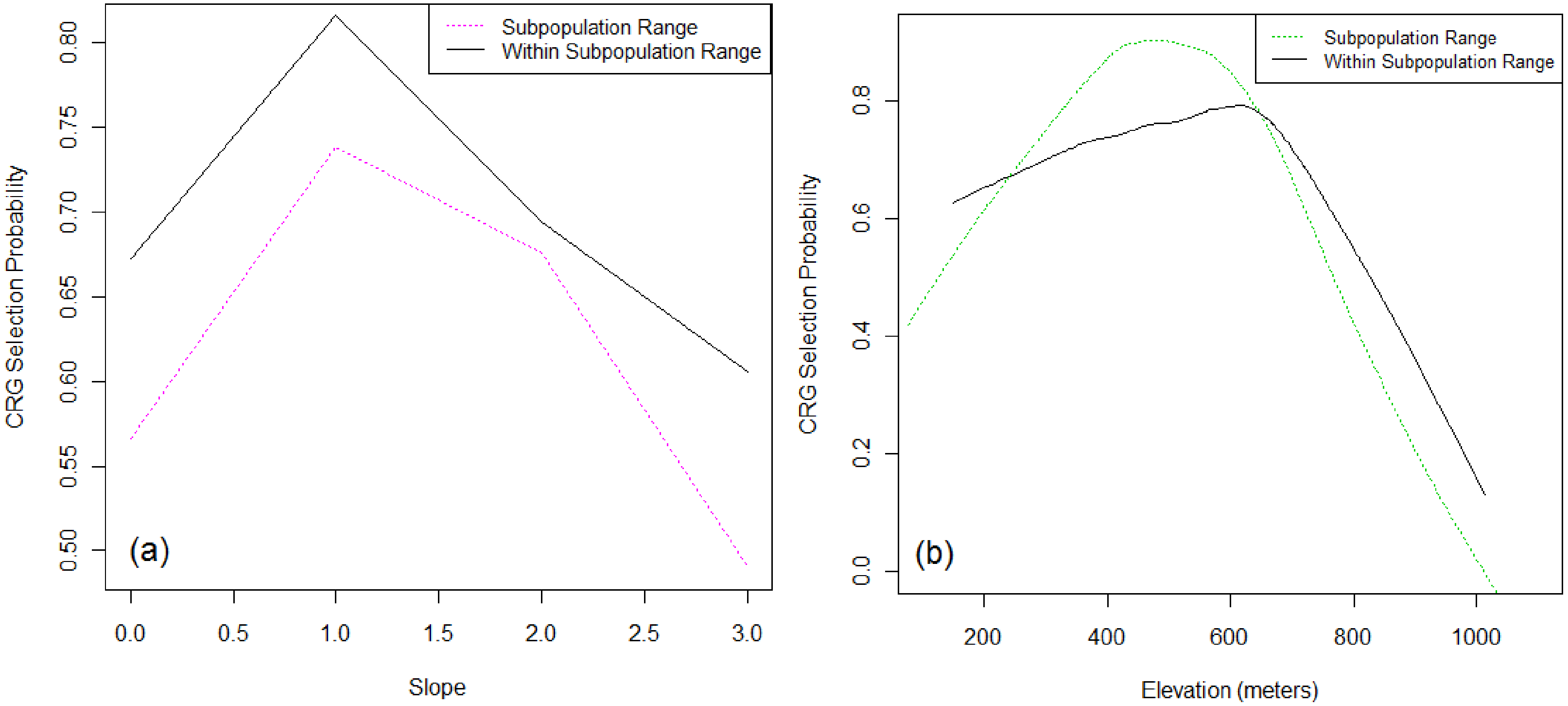


Figure 2. Habitat selection probabilities for Cross River gorillas in response to (a) available slope and (b) elevation reveal similar non-linear patterns at both the subpopulation range (i.e., landscape) scale and at a finer within-range scale.

Figure 3.

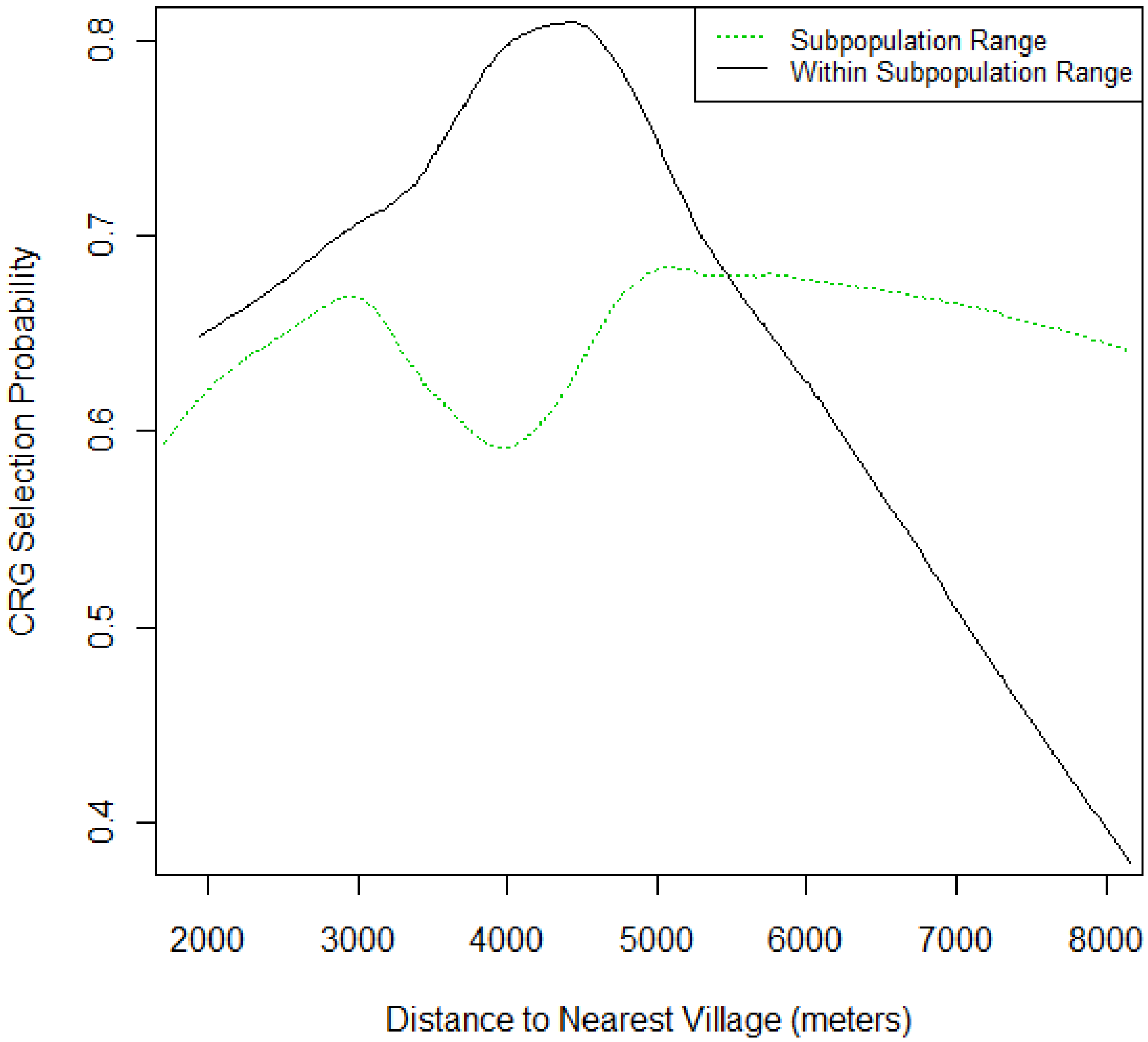


Figure 3. Probability of habitat selection by Cross River gorillas in relation to distances from the nearest village. Distance to nearest village was not a significant predictor of selection at the subpopulation range/landscape scale, but habitat selection within range showed significant selection of sites at intermediate distances from villages.

Figure 4.

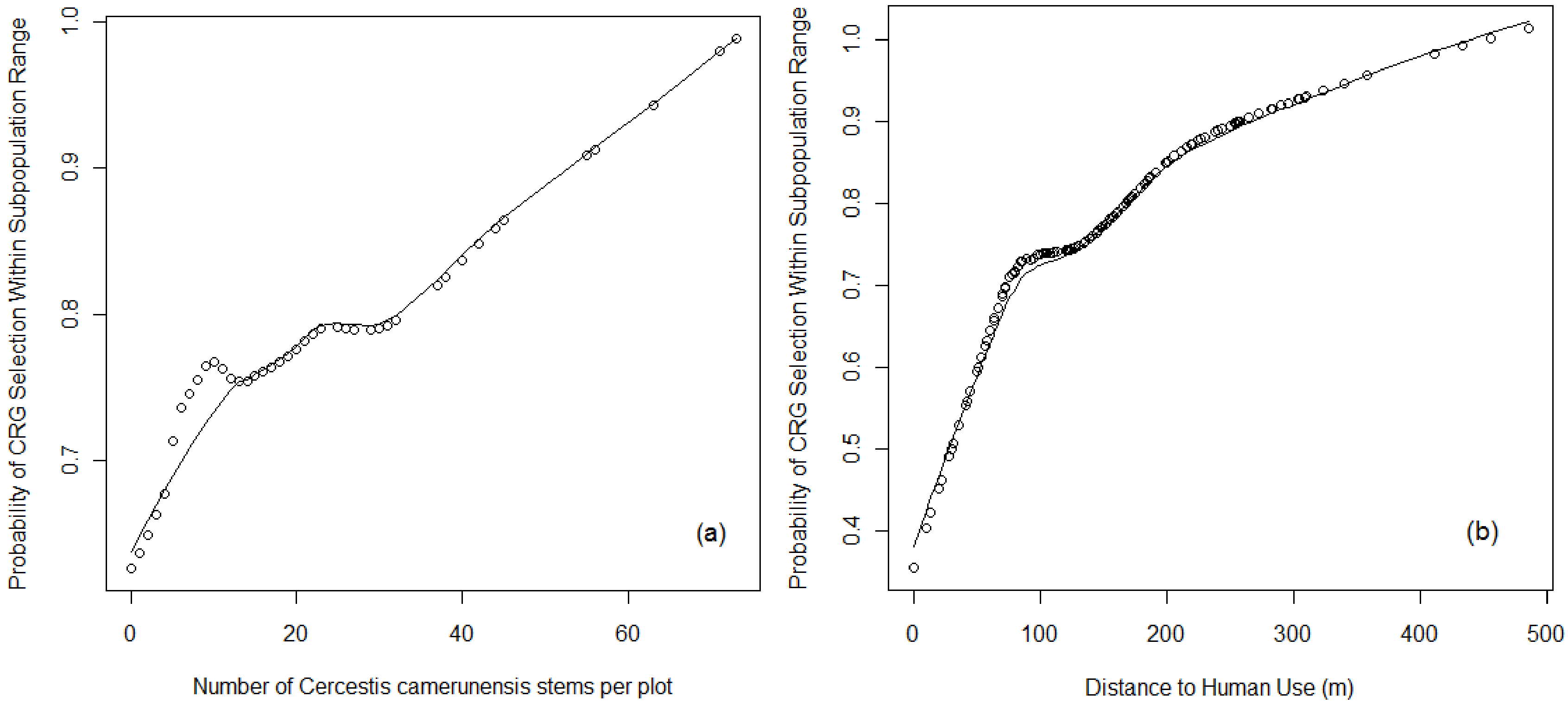
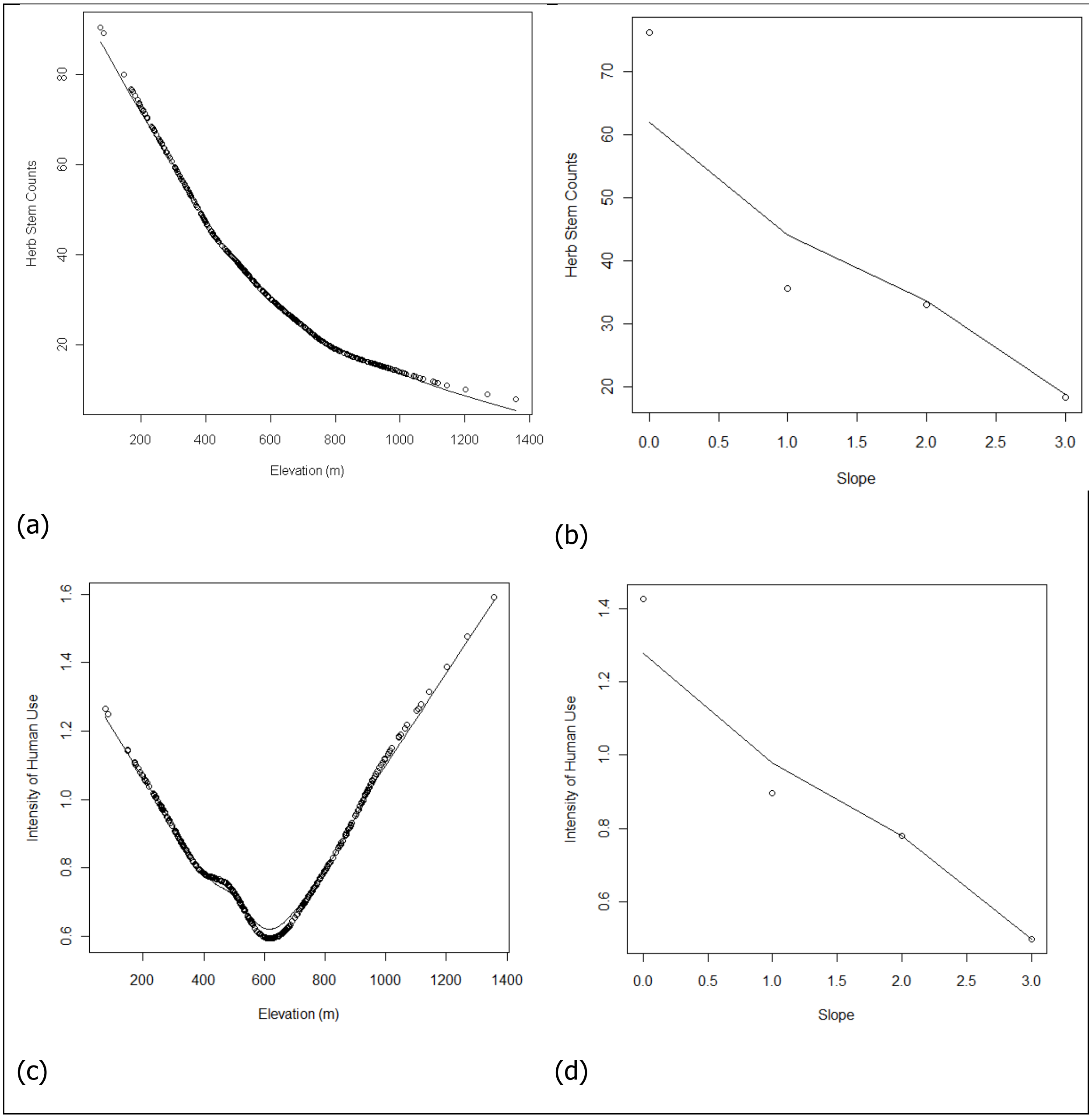


Figure 4. Probability of habitat selection within the Cross River gorilla subpopulation range in relation to (a) availability of the most preferred food species and (b) distance to human activities

Figure 5.



(a)

(b)

(c)

(d)

Figure 5. Availability of herbaceous plants preferred by Cross River gorillas was negatively correlated with both (a) elevation and (b) slope. Intensity of human activities had a significant and non-linear relationship with elevation (c) and was negatively correlated with slope (d)

CHAPTER 6

General Conclusions and Future Directions

This study highlights the utility of integration of ecological and anthropogenic data across multiple scales to inform management strategies. A different picture of critical habitat for the Cross River gorilla (CRG) is presented with each progressively finer scale of resource selection, and together these scales produce a more complete understanding of relationships between species distribution and behavior. Our study suggests that both remotely-sensed habitat type and distance from villages may be poor proxies for the landscape variables influencing CRG habitat use in Cameroon. Assuming that steep slope, high elevation locations are highly suitable features and desired by CRG may not be correct, and this could negatively influence connectivity conservation efforts. Conservation decisions assuming that CRG will use protected habitat if its high elevation and covered with forest, may end up protecting unsuitable habitat due to low food availability, and moreover, not protecting habitat that could be important. Instead, conservation planning designed to ensure persistence of CRG subpopulations requires a closer look at staple food availability and human activities throughout the landscape to determine what proportion of remaining forest represents unsuitable versus suitable but unoccupied habitat, and to inform protection of critical habitat areas.

CRG habitat management in both Cameroon and Nigeria will likely be more successful with a better understanding of how important food species help maintain CRG subpopulations and the tradeoffs CRG make between food availability and risk of human contact. CRG live in fragmented subpopulations, and the selection by the CRG of areas with high availability of preferred foods indicates that maintaining connectivity will likely require protection of habitats that contain preferred food species. Given that herbs are a keystone resource for gorillas and can serve as an important buffer when fruit is scarce, high availability of preferred herb species like *Cercestis camerunensis, Palisota spp,* and *Aframomum spp* may indicate areas of great conservation value for CRG. In the Mone/Mt. Oko area, slope and elevation appear to have negative correlations with abundance of *Palisota, Aframomum*, and *C. camerunensis,* highlighting the potential importance of lower slope and elevation sites for the viability of CRG populations. Additionally, even within the CRG's small geographic range, diet may vary greatly. Further research will be necessary to better understand possible differences in food availability, diet, and food preference among the remaining subpopulations.

Longer term, more in-depth studies of CRG diet, including phenology and explicitly examining fruit in the diet, will be necessary to get a complete picture of CRG dietary ecology. Such studies are underway within some CRG subpopulations, and should be expanded to include additional areas.

Spatial delineation of CRG subpopulations is also critical to understanding CRG habitat requirements and to target conservation actions. However, choice of home range method will ultimately depend partly on study purpose, study scale, and amount of data the researcher is able to collect. For patchily distributed species like the CRG, where limited data exist but immediate conservation action is necessary, the strengths and weaknesses of each home range modeling technique should be carefully considered. Therefore, if study goals include providing evidence for the protection of the maximum possible area for the CRG, Kernel estimates are recommended. Thus, in many regions of Nigeria and areas like Kagwene in Cameroon, where rates of forest loss are high and remaining suitable habitat is already severely limited, Kernel methods may be most useful. However, both for attempts to determine geographic or anthropogenic barriers to CRG habitat use or movement and for analyses of the subpopulation patterns at fragmented scales, this study suggests that Local Convex Hull (LoCoH) may prove to be the best method. It must nevertheless be noted in such studies that the LoCoH 100% isopleth is likely to be an underestimate of the true space required by the subpopulation. Conservation planners must take this underestimate into account when delineating critical habitat, and perhaps consider applying a combination of modeling methods.

Different conservation decisions will need to take into account different scales of analysis. Protected area design may be best informed by CRG home range selection scales and patterns of land claims and land use by local villages. On the other hand, multiple-use planning for matrix areas to maintain connectivity may be more effective using fine scale selection informing individual day-to-day movement of both gorillas and people to ensure that obstacles to CRG survival and connectivity do not increase in the landscape. This will require large-scale data collection to assess food availability and human use over the landscape, and to then predict suitability/connectivity based on this information. While a large-scale, data-intensive study may be expensive and logistically difficult, it will likely prove critical for gaining a deeper understanding of CRG niche ecology while informing habitat conservation planning in the face of land-use and land-cover change in the region.

The subtleties of sustainable and compatible human landscape uses in this system remain unclear and must be explored further. There may be thresholds of human activity above which gorillas will not use habitat, and thresholds of herbaceous food availability below which they will not select habitat. This will have major implications when deciding how best to protect habitat with multiple uses, protect human livelihoods, and protect critical CRG resources at the same time. More research is needed on human harvest levels and traditional activities that will be congruent with

CRG use in food-rich areas. Additionally, education about compatible human landscape uses may be more effective than simple protected area demarcation, which has engendered negative feelings towards conservation recently in this area.

Conservation priorities in the CRG range must be adjusted to overcome current obstacles to effective implementation. First, communication is an essential part of any conservation program; in addition to international NGOs and national governments, local populations, in both Cameroon and Nigeria, must have a stake in the development, management, and review of conservation projects in the CRG landscape. Conservation programs must also work to rectify discrepancies in immediate local economic interests, with a view to providing long-term social and global benefits. This will involve targeted capacity building, so that conservation efforts grow from the bottom up, developing with the local populations rather than in spite of them. This capacity building is needed at all levels of involvement: legislative development, enforcement, management, research, and outreach. It is "necessary to empower local populations to as great an extent as possible, and to give official recognition to this empowerment" (Global Environment Facility 2003). Engendering local pride and ownership in conservation initiatives will be a key to success in this landscape. Local involvement in the Afi Mountain Wildlife Sanctuary and the Kagwene gorilla sanctuary may be important steps towards this local ownership, but further efforts on a larger scale are necessary. Successful conservation endeavors will also require more directly linking sustainable economic development programs to conservation goals and clarifying the interconnectedness of resource harvest, livelihoods, and biodiversity conservation.

Second, CRG conservation will require sustainable, long-term funding. Successful examples of sustainable funding initiatives to explore further can be found in Mountain gorilla conservation programs in East Africa. In Uganda, initial Global Environment Facility (GEF) funding has been used to create self-sustaining tourism, conservation, and development programs in gorilla habitats. The Bwindi Mgahinga Conservation Trust (BMCT) was established in 1995 to support biodiversity conservation in Bwindi Impenetrable National Park (BINP) and Mgahinga Gorilla National Park (MGNP) in perpetuity by investing seed money donated from the GEF, USAID, and the Royal Netherlands government. The fund is used for community development projects, research, and park enforcement costs, and has even been used to purchase land from local communities and give it to displaced Batwa people to resettle. The hope is "[t]o foster conservation of the biodiversity of MGNP and BINP through investments in community development projects, grants for research and ecological monitoring, funding park management and protection and programmes that create greater conservation awareness" (Bwindi Mgahinga Conservation Trust 2010). The Conservation Development Centre prepared a 10-year performance review of the BMCT, and found that "the BMCT has overall been highly successful in delivering its field programme and has been instrumental in generating increased support and capacity for natural resources conservation in the Bwindi-Mgahinga area" (Conservation Development Centre 2009). With the development of this trust, and the collaboration of various

NGOs, Uganda has created a flexible and integrated national program. Creating similar, but locally tailored, funding programs in Cameroon and Nigeria may prove invaluable in the future of CRG conservation.

Finally, consistency, standardization, and adaptive strategizing across local and national borders will be necessary for successful conservation of the Cross River gorilla. This must first entail standardizing and collating existing data in a central system. It will then involve outlining long-term research and adaptive management goals and programs to reach those goals. It will be critical to track changes, successes, and setbacks in these management programs, and finally to adapt and evolve these strategies as more data become available and the political climates change. Working collaboratively transnationally and across stakeholders will permit future successes in CRG conservation.

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Appendices

Appendix 1. Plant species eaten by Mone Subpopulation of Cross River gorillas. Species in bold were most frequently observed and, when combined, made up half of observed feeding signs

Family	Species	Life Form	Parts Eaten
Acanthaceae	*Acanthaceae sp 1*	herb	leaves, pith
	Acanthaceae sp 2	herb	leaves, pith
	Acanthaceae sp 3	herb	leaves, pith
	Acanthaceae sp 4	herb	leaves
	Acanthus montanus	herb	leaves
Amaryllidaceae	*Amaryllidaceae sp*	herb	leaves, pith
Anacardiaceae	*Antrocaryon klaineanum*	tree	fruit
	Pseudospondias microcarpa	tree	leaves, fruit
Annonaceae	*Cleistopholis patens*	tree	leaves
	Enantia chlorantha	tree	leaves
Apocynaceae	*Alstonia boonei*	tree	leaves
	Landolphia sp	**liana**	**leaves, fruit, bark**
	Rauvolfia vomitoria	tree	leaves
	Voacanga sp	tree	leaves
Araceae	*Anchomanes difformis*	herb	pith
	Anubias sp	shrub	leaves
	Cercestis camerunensis	**herb**	leaves**, pith**
	Nephthytis sp	herb	leaves, pith
	Stylochaeton zenkeri	**herb**	**leaves**
Balsaminaceae	*Balsaminaceae sp*	tree	leaves
Bignoniaceae	*Markhamia sp*	tree	leaves
Burseraceae	*Santiria trimera*	tree	leaves, pith, root
Cecropiaceae	***Musanga cecropioides***	**tree**	**leaves**, pith, bark
	Myrianthus arboreus	tree	bark
Celastraceae	*Salacia sp*	tree	leaves, bark
Commelinaceae	*Commelina sp*	herb	leaves, pith
	Palisota sp 1	**herb**	**leaves, pith**
	Palisota sp 2	herb	pith
Convolvulaceae	*Ipomea sp [hederifolia?]*	liana	leaves, pith
Euphorbiaceae	*Drypetes sp*	tree	leaves
	Uapaca guineensis	tree	young leaves, pith
Fabaceae	*Leonardoxa sp*	tree	pith

Guttiferae	*Garcinia ovalifolia*	tree	leaves
Icacinaceae	*Lavigeria sp*	tree	young leaves
	Leptaulus sp	tree	leaves
Irvingiaceae	*Klainedoxa gabonensis*	tree	fruit
Lecythidaceae	*Napoleonaea sp*	tree	leaves
Leeaceae	***Leea guineensis***	**tree**	leaves, **fruit**, pith
Leguminoseae	*Anthonotha macrophylla*	tree	leaves
Malvaceae	*Cola sp (cimicapaphila?)*	tree	fruit
	Cola clamydiantha	tree	fruit
	Cola lepidota	tree	fruit
	Cola millenii	tree	leaves
	Desplatsia sp	tree	leaves
Marantaceae	*Hypselodelphys sp*	herb	pith
	Marantaceae sp 5	herb	pith
	Marantochloa purpurea	herb	pith
	Megaphrynium sp	herb	pith
	Thaumatococcus sp	herb	leaves
Miliaceae	*Guarea thompsonii*	tree	leaves
	Trichilia rubescens	tree	leaves, bark
Menispermaceae	*Penianthus sp.*	tree	fruit
Mimoceae	*Parkia bicolor*	tree	fruit
Moraceae	*Dorstenia sp 1*	tree	leaves, bark
	Dorstenia sp 2	tree	leaves
	Ficus sp	tree	leaves, pith, bark
	Milicia excelsa	tree	leaves
	Trilepisium madagascariense	tree	leaves, fruit, pith, bark
Myristicaceae	***Pycnanthus angolensis***	**tree**	**leaves**, pith, bark
	Staudtia kamerunensis	tree	leaves
Palmae/Arecaeae	*Eremospatha macrocarpa*	tree	pith
	Eremospatha wendlandiana	tree	pith
	Laccosperma opacum	**tree**	**pith**
	Oncocalamus sp	tree	pith
	Raphia sp.	tree	pith
Phyllanthaceae	*Protomegabaria sp.*	tree	leaves, pith, bark
Piperaceae	*Piper umbellatum*	herb	leaves, pith
Rubiaceae	*Canthium sp*	tree	pith, bark
	Heinsia crinita	tree	leaves
	Mussaenda sp	tree	leaves
	Pavetta sp	tree	leaves
	Psychotria sp	shrub	leaves
	Rubiaceae sp	liana	pith
	Tetraceras sp	liana	pith

Sapotaceae	*Synsepalum sp*	tree	leaves
	Gambeya sp.	tree	leaves
Sterculiaceae	*Cola sp. 5*	tree	leaves
Thymelaeaceae	*Dicranolepis sp*	tree	leaves, bark
Unknown	*Unknown liana 1*	liana	base
	unknown liana 10	liana	leaves
	Unknown liana 2	liana	pith
	Unknown liana 3	liana	pith
	Unknown liana 4	liana	leaves
	Unknown liana 5	liana	leaves
	Unknown liana 6	liana	leaves
	Unknown liana 7	liana	bark
	unknown liana 8	liana	pith
	Unknown liana 9	liana	leaves
	Unknown shrub 1	shrub	leaves
	Unknown herb 1	herb	bark
	Unknown tree 1	tree	leaves
	Unknown tree 2	tree	leaves
	unknown tree 3	tree	leaves
	unknown tree 4	tree	leaves
Urticaceae	*Urera rigida*	liana	leaves, pith, root
Verbenaceae	*Clerodendron sp*	tree	pith
Violaceae	*Rinorea oblongifolia*	tree	leaves
Vitaceae	*Cissus aralioides*	liana	pith, bark
Zinziberaceae	***Aframomum sp 1***	**herb**	leaves, **pith**
	Aframomum sp 2	herb	pith
	Aframomum sp 3	herb	pith
	Costus afer	herb	leaves, pith

Appendix 2.

Background information for the desert bighorn sheep case study on LCP methods.

Methods and background for the Epps et al. (2007) "Optimized" least-cost model

Epps *et al.* (2007) conducted their study in the Mojave and Sonoran Desert regions of California, where desert bighorn sheep typically inhabited small mountain ranges isolated by flat desert with little water and limited forage. They estimated gene flow among 26 populations (392 individuals) using 14 microsatellite loci. Epps et al. (2007) used a matrix-based regression approach to test whether gene flow among populations of desert bighorn sheep varied as a function of distance and topography or distance alone, and to identify which model of distance and topography best approximated the effect of these variables on gene flow. Topography was defined as slope greater than 5%, 10%, or 15%, depending on the model tested. Slope was estimated from a 30 m DEM; slope values were then resampled to 90 m cells to improve calculation speed. Because bighorn sheep use steep slopes to escape predators, slopes greater than those cut-off values ("slope cells") were modelled as having lower resistance than cells with slopes less than the cut-off values ("not slope cells). For each slope cut-off value tested, a series of models was created with different relative resistance values for slope or "not slope" cells.

Model optimization proceeded as follows: first, Epps *et al.* (2007) calculated a series of matrices ($\mathbf{X}_1$-$\mathbf{X}_i$) of effective distances (ED) among populations, where each matrix represented estimates of ED between all population pairs based on a unique set of parameter values (i unique combinations) for slope cut-off value and resistance values for "slope" or "not slope" cells. Next, a matrix (**Y**) depicting the presence or absence of anthropogenic barriers (fenced highways, canals and urban areas) among those 26 populations was generated to control for the effect of those barriers on gene flow (Epps et al., 2005). Finally, a matrix (**Z**) of gene flow estimates between all population pairs was developed (*Nm*, or *M* as estimated using program MIGRATE (Beerli & Felsenstein, 2001)). They used partial Mantel tests to assess the correlation of **Z** (gene flow) with each matrix $\mathbf{X}_i$ (ED), while controlling for the effect of **Y** (anthropogenic barriers). In that manner parameter values for the ED model resulting in the strongest correlation between **X** and **Z** were identified. That exercise was repeated using three different methods to define the geographical extent of each population, as well as a second method of estimating gene flow, to examine how sensitive model fitting was to those variables. The optimized model of ED was then used in later analyses of corridor length and location.

Maximum effective distance was determined by plotting estimates of gene flow against effective distance, fitting a curve using non-parametric regression, and then approximating that curve with a negative exponential function for predictive purposes. Maximum corridor length was defined as the point where the non-parametric regression fit first stopped decreasing (see Epps *et al.* 2007 for more detailed explanations).

San Gorgonio and Cushenbury bighorn sheep populations

The Cushenbury population of desert bighorn sheep was first discovered in the 1980s (J. Davis, California Department of Fish and Game, personal communication) and was thought to have resulted from a recent colonization. That population contained 25-50 individuals during genetic sampling in 2002-2003. Epps *et al.* (2010) determined that the source of the colonization was the nearby San Gorgonio population, based on analyses of microsatellite markers and mitochondrial DNA.

Population polygons for LCP modeling for those populations were defined by Epps *et al.* (2007) based on radiotelemetry locations (CDFG, unpublished data; monthly locations are derived from males and females totaling 7 individuals over 1 year (San Gorgonio), and 25 individuals over 8 years (Cushenbury)). They used a fixed kernel density estimator (Beyer, 2004) to define the 95% density kernel, and increased the amount of smoothing until a single 95% density polygon was achieved for each population.

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Appendix 3: Recommendations for effective LCP modelling

Source patches should accurately represent populations of interest

- Collect enough data to conduct home range analysis appropriate to species in question
  - E.g. Minimum Convex Polygon, kernel density estimator, local convex hull, grid squares
- Use local knowledge to determine where, within protected areas or habitat patches, animals are known to occur
- Avoid using entire protected areas or forest patches as source patches unless data suggest the population in question actually uses entire area

Included variables should reflect species (not researcher) view of landscape

- Find significant predictors of species habit selection
  - E.g. habitat suitability analysis, resource selection function, behavioural observations
- Find significant predictors of species movement patterns
  - Use radiotelemetry or direct behavioural observations where possible to analyze speed and/or direction changes at identifiable landscape elements
- Explicitly identify biological process of interest to justify chosen variables and cost scheme development

Study grain should reflect perception of species in landscape

- Determine optimal pixel size with behavioural/ecological studies
  - E.g. day travel length, distance between resting/feeding sites, distance at which animals respond to conspecific or interspecific playbacks, radiotelemetry data on migration or dispersal movements, territory or home range size, measured inter-patch movements
- Ensure available data (e.g. remotely sensed land-cover classification) accurately reflects movement/use predictors (e.g. predator/prey abundance, movement speed, etc.) through regression analysis

Researchers should optimize cost schemes with empirical data and perform model validation

- Split species occurrence data into two groups: use half as training set and half for model validation
- Use genetic and behavioural data where possible
- Utilize local/indigenous knowledge where appropriate
- Continue to collect data on species movement/landscape use after initial LCP analysis recommendations are made

Researchers should perform standardized sensitivity analysis and model selection

- Test sensitivity of model outcomes to the choice of habitat factors, factor weights, resistance values, grain, and definitions of both patches and least cost corridors
- Test sensitivity of model outputs, particularly placement and resistance of potential corridors, to uncertainty of inputs using point estimate, minimum, and maximum values for factor weights and resistance values (as recommended by Beier *et al.* 2009)
- Estimate uncertainty and error rates associated with land cover classification where applicable

One-pixel wide least cost path should not be final output of LCP analysis

- Determine if least-cost path is useable by species of interest
  - Determine maximum effective distance species is likely to travel
    - E.g. model gene flow measures, dispersal data, home range size, as functions of effective distance
- Move beyond single-pixel wide paths to more biologically relevant least-cost corridors
  - E.g. buffer to acceptable width, take lowest percentage of cost surface to create likely dispersal zone
- Give managers multiple low-cost options so that they can take into account social and economic factors before choosing optimal linkage placement

Appendix 4: A Note on Variation in Least Cost Terminology

The published literature has not yet come to a consensus on least-cost path (LCP) analysis terminology. More publications use the term ‘least-cost path’ analysis than any other term, as a general term both for analyses of single paths and approaches that extend that methodology (e.g. to least-cost corridors). Nineteen of forty-one recent studies use ‘least cost path’ analysis. On the other hand, many studies also either refer to LCP analysis as ‘least-cost’ modelling (fifteen of forty-one), or ‘cost distance’ modelling (seven of forty-one). I chose the most common terminology for this review, but I highlight the variation in terminology employed. This is just one example of the current lack of standardization in LCP analysis.

Appendix 5. Full summary of recent studies that used least-cost path (LCP) modelling for habitat connectivity design

Study	**Focal Species**	**Variables Included[6]**	**Scale[7]: Grain m^2 / Extent km^2**	**Source of Cost Schemes**	**Source Patches**	**Adjacent habitat[8]**	**Cost Value Ranges**	**Validation**	**Sensitivity Analysis**	**Path to Corridor[9]**
Beazley *et al.* 2005	American moose (*Alces alces*), American marten (*Martes americana*), Goshawk (*Accipiter gentilis*)	Forest cover (3); road density	200 / 48800	Habitat suitability index (HSI) map based on species presence; literature & expert opinion	All 'suitable' habitat patches (HSI)	No	Unknown	Presence/ absence of dung (moose only)	No	Minimum width: 1 km (marten); 10 km (moose)
Chetkiewicz & Boyce 2009	Grizzly bear *(Ursus arctos)* & cougar (*Puma concolor)*	Land cover (5); sub-region; food resources; terrain; road density	900 / 425 & 1657	Resource selection function (RSF) based on telemetry locations	High RSF value polygons	No	Inverse of RSF coefficients	Telemetry locations; (spearman rank, chi-square, linear regression)	No	Buffered to 350 meters
Cushman *et al.* 2008	American black bear (*Ursus americanus*)	Land cover (26); elevation; slope; roads	8100 / 3000	Molecular genetics; literature, knowledge of species	Individual animal locations;	No	1-10	Genetic distance (Mantel test)	No	Smoothed to with 2500 m radius parabolic kernel
Driezen *et al.* 2007	Hedgehogs (*Erinaceus europaeus*)	Land cover type (12); roads; water	100 / 84.73	Literature/ previous studies	Unknown	No	1 (pasture) - 1000 (large road)	Experimental dispersal data	Compared 12 sets of costs	No

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[6] Number of cover/type categories is indicated in parentheses

[7] Grain of study is the cell/pixel size, or highest level of resolution (measured in square meters);
Extent is the size of the entire study area (measured in square kilometers)

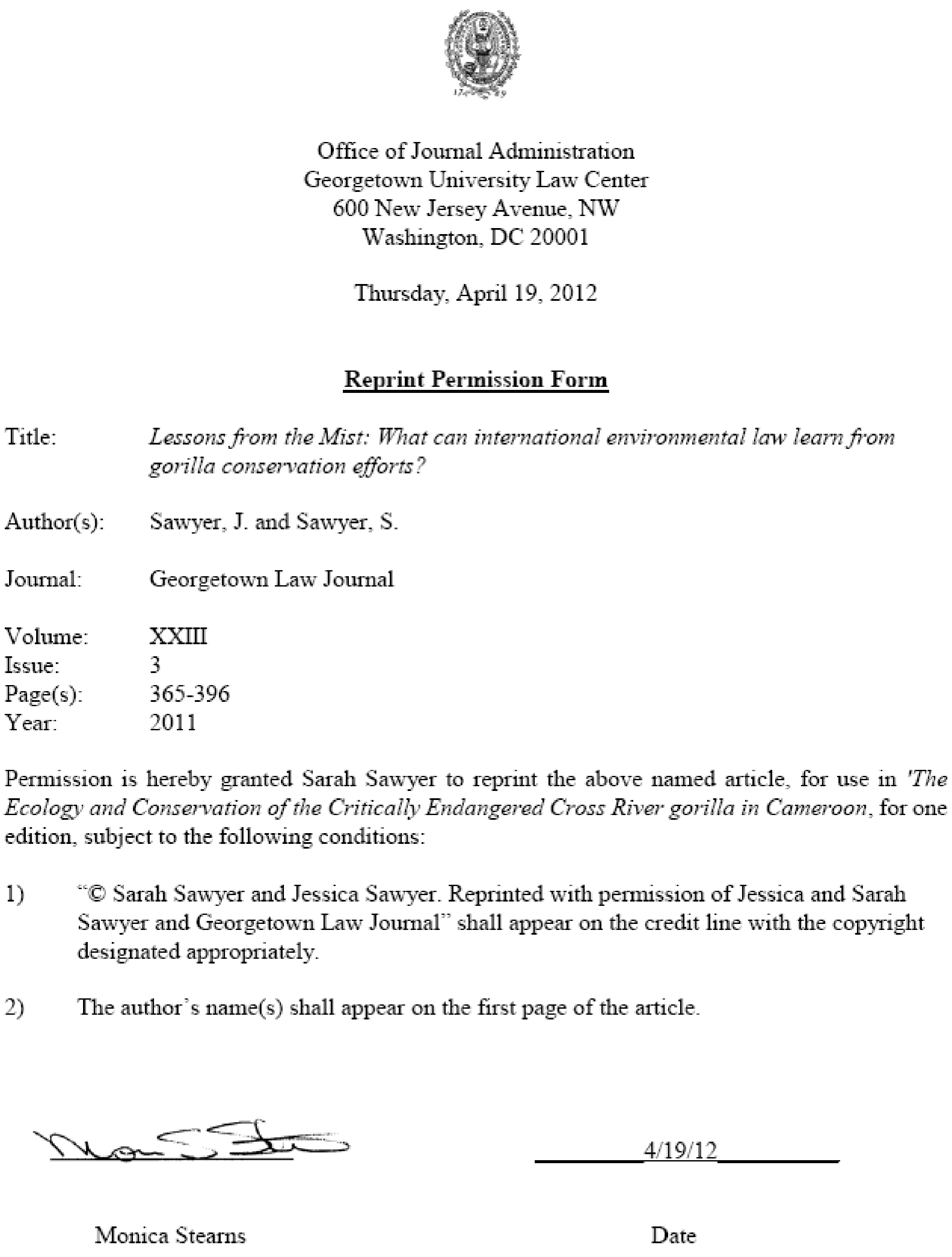
[8] Did study consider adjacent habitat characteristics when determining resistance of cell?

[9] Did study go beyond least-cost path (LCP) to make a more biologically relevant recommendation, or least-cost corridor (LCC)?

Epps *et al.* 2007	Desert bighorn sheep (*Ovis canadensis nelsoni*)	Slope (2); distance; barriers	10000 / Unknown	Genetics – (partial Mantel tests); radio-telemetry presence data	3 polygons: minimum convex; suitable habitat; expert opin.	No	0.1(>15% slope); 1(<15% slope)	Radio-telemetry data	Compared multiple measures of gene flow	No
Hepcan *et al.* 2009	Hyaena (*Hyaena hyaena*), lynx (*Lynx lynx*), jungle cat (*Felis chaus*), caracal (*C. caracal*)	Vegetation type (12); road density	100 / 18.905	Expert opinion, literature	'Key Biodiversity Areas'	No	Unknown	No	No	Minimum width: 1 km
Joly *et al.* 2003	Toad (*Bufo bufo*)	Habitat type (7); roads; rivers	100 / 56.3	expert opinion, literature	Unknown	No	Habitat type: 5-80; road mortality risk: 0-1	No	No	No
Kautz *et al.* 2006	Florida panther (*Puma concolor coryi*)	Land cover (16)	900 / 60256	Radiotelemetry (compositional and Euclidian distance)	Home ranges (kernel) & potential habitats (HSI)	No	land cover: 1-11; water: 15; road: 20	No	Partial: road & water; sensitivity not detected	Post-analysis buffer
Kindall & Van Manen 2007	American black bear (*Ursus americanus*)	Forest cohesion, diversity, & forest-agricult. edge density	200000, 7.1 million, & 38.5 million / 120	Probability of occurrence model: presence data	50% fixed kernel home ranges	No	1 -8 (ranked possible combination of 3 habitat variables	No	No	No
Kong *et al.* 2010	Generic urban wildlife species	Land use type (12)	100 / 538	Expert opinion	Urban green spaces larger than 12 ha & connected to areas outside city	No	0.1 (scenery forest) - 50,000 (construction area)	No	No	No
Larkin *et al.* 2004	American black bear (*Ursus americanus floridanus*)	Habitat class (5) based on suitability model	900 / 689	Expert opinion, literature	'Suitable' habitat (expert opinion)	No	1 (core); 10 (tolerated)50 (human impacted); 100 (barrier)	No	Two cost schemes: 1-4; & 1, 100, 500, 1000 sensitivity detected	No (but conducted bottleneck analysis)

LaRue & Nielsen 2008	Cougar (*Puma concolor*)	Land cover (8); distance to road & water; slope, human pop. density	8100 / 3182294	Expert opinion survey (Analytical Hierarchy Process)	Areas where cougar may be living (expert opinion)	Distance to road & water	0.19 - 1.92 (for 3-8 categories per variable)	No	No	Buffered LCP by 1 km
Li *et al.* 2010	Giant panda (*Ailuropoda melanoleuca*)	Land cover type (9),slope; distance to water & human activities (roads; farms; residential areas)	Unknown / 2000	Expert opinion surveys (Analytical Hierarchy Process)	Source points: panda occurrence or suitable habitat	Distance to various human activities	Reciprocal of habitat suitability: 0.002 (highly disturbed) - 0.098 (bamboo)	No	No	Smoothed with cumulative kernel across path points (90 m apart)
Meegan & Maehr 2002	Florida panther (*Puma concolor coryi*)	Habitat type (2); roads	900 / 9235.76	Expert opinion literature, radio-telemetry	forest patches 500 hectares or larger	No	1,2, or 3	presence locations	No	No
Osborn & Parker 2003	African elephant (*Loxodonta africana)*	Habitat suitability (2); dist. to river, roads, & settlements	Unknown / 6000	Expert opinion	Individual locations (telemetry)	Distance to settlements & roads	Unknown	No	No	No
Rabinowitz & Zeller 2010	Jaguar (*Panthera onca)*	Land cover; percent tree & shrub cover; elevation; distance to roads & settlements; human pop. density	1000000 / 4 million	Expert opinion survey (averaged reported costs)	Jaguar conservation units: 90 known populations of jaguars)	Distance to roads and settlements	Integers 0-10	Currently conducting occupancy modelling through field interviews	No	Selected lowest 0.1% of grid cell values; corridors < 10 km wide are 'of concern'
Rouget *et al.* 2006	African elephant (*Loxodonta africana)*	'Suitability' (foraging model)	1000000 / 105454	Unknown	Unknown	No	Suitability: 0 (high); 300 (med); 600 (low); 900 (not)	No	No	Buffered to 1 km
Schadt *et al.* 2002	Eurasian lynx (*Lynx lynx*)	Land cover (5); roads	1000000 / 374000	Expert opinion; literature	Areas of 'suitable' habitat according to size, isolation, & forest cover	No	1 (forest) - 1000 (urban or water)	No	Partial: varied 'matrix' cost 4-500; sensitivity detected	No

Shen *et al.* 2008	Giant panda (*Ailuropoda melanoleuca*)	Land cover; bamboo cover; elevation; slope, aspect; distance to residential areas & road	900 / 43623	Expert opinion (Delphi method-analytical hierarchy process)	'Core' habitats based on land cover type	Distance to residential areas & roads	1-50	No	Partial: varied cost of land & bamboo cover; sensitivity detected	No
Singleton *et al.* 2004	Grizzly bear (*Ursus arctos*)	Land cover (13); road density; human pop. density; slope	8100 / 325667	Expert opinion; literature	Largest areas of low human influence with suitable land cover	No	0.1-1.0	No	No	Took lowest 10% of cost surface
Stevens *et al.* 2006	Natterjack toad (*Bufo calamita*)	Land cover (6); water	09 / 98	Experimental movement behaviour	Minimum convex polygons of toad populations	No	3 models: Euclidian: all costs 1; Resist.: 8.2-10000; Pref.: 41.18-10000	Genetic dispersal rates (Mantel test)	Compared multiple measures of gene flow	No
Wang *et al.* 2008	Spiny rat (*Niviventer coninga*)	Normalized difference vegetation index; slope; aspect; distance to land types	100 / 100	Ecological niche factor analysis (HSI) on presence data (trapping)	Individual animal locations	distance to land types of differing human influence	1-1,000	Presence (k-fold cross validation of data set); Gene flow	No	No
Wang *et al.* 2009	California tiger salamander (*Ambystoma californiense)*	Vegetation type (3)	1 / 10	Expert opinion; presence data	Breeding pair locations	No	1-10	Gene flow estimates	No	No
Wikramanayake *et al.* 2004	Tiger (*Panthera tigris*)	Habitat type (3); elevation; land cover in buffer area (5); patch size	Unknown / unknown	Expert opinion; previous studies	Unknown	Cell within 1 km of agriculture or pop. centre = 'poor habitat'	1-25	No	No	Selected 10%, 20%, and 30% of grid cells with lowest cost values



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