SCRATCHING THE SURFACE: A CONTENT ANALYSIS OF GORILLAS AS ZOOGEOMORPHIC AGENTS

by

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LIST OF ABBREVIATIONS

Abbreviation **Description**

CAR – Central African Republic
CR – Critically Endangered
D-N.N.P. – Dzanga-Ndoki National Park
DRC – Democratic Republic of the Congo
D-S.D.F.R. – Dzanga-Sangha Dense Forest Reserve
IUCN – International Union for Conservation of Nature and Natural Resources
ITCZ – Intertropical Convergence Zone
K-B.N.P. – Kahuzi-Biega National Park
K.G.S. – Kagwene Gorilla Sanctuary
L.R. – Lopé Reserve
N-N.N.P. – Nouabale-Ndoki National Park
ROC – Republic of the Congo
SA – South Africa
Vi.N.P. – Virunga National Park

ABSTRACT

Gorillas are among the most charismatic and well-researched species on the planet, yet their role as zoogeomorphic agents has gone largely overlooked. Zoogeomorphology is the study of animals as geomorphic agents, that is, their role in sculpting, modifying, and maintaining the earth's physical surface. Documented gorilla zoogeomorphic activity is scattered within the literature of various disciplines and functions mostly as supplementary data to primary research goals. Knowledge on the geomorphic responses of gorillas is necessary to refine our understanding of their role as present and future agents of landscape formation and decay. Without zoogeomorphic data, vital pieces of information could be excluded in future conservation planning. This study is a content analysis of non-human primate literature that utilizes a conventional approach to identify, categorize, and define cases of gorilla zoogeomorphic activity. Nine categories of how gorillas function as zoogeomorphic agents have been identified. They include: (1) soil scratching and (2) soil scraping of the forest floor; (3) excavated chambers and depressions; (4) bare/semi-bare soil nest sites; (5) hand/knuckle and foot prints; (6) excavated insect mounds; (7) geomorphic implications of tool use (8) trunk uprooting, and (9) trampling. Data sets derived from the literature were used to provide a qualitative and quantitative summary of zoogeomorphic activity. Descriptive statistics were used to quantify literature reports and key zoogeomorphology studies were used to extrapolate potential trace specific geomorphic response(s).

I. INTRODUCTION

The ridge supporting numerous trees had been so dug out by the gorillas that the tree roots formed exposed gnarled supports for the vast caves created by the animals' repeated soil digging. It was eerie to watch the huge silverback magically disappear beneath a web of tree roots into total blackness. When he emerged, covered with the sandy crumbs of his feast, he moved off, leaving the cavern to the other group members. In order of rank, they disappeared into its depths. Their subsequent screams and pig-grunts reflected the overcrowded conditions.

~ Dian Fossey (1983, 52-53)

Gorillas (*Gorilla spp.)* are among the most charismatic and well-researched species on the planet, yet their role as zoogeomorphic agents has gone largely overlooked. Zoogeomorphology (Butler 1992) is the study of animals as geomorphic agents, that is, their role in sculpting, modifying, and maintaining the Earth's physical surface. This study identified nine categories of gorilla zoogeomorphic activity which include (1) soil scratching (with hands) and (2) scraping (with incisors) of the forest floor; (3) chambers and depressions created from surface excavation; (4) bare and semi-bare soil nest site constructions; (5) insect mound excavation; (6) trampling; (7) hand/knuckle and foot prints; (8) surface disturbance as a result of tool use; and, finally, (9) trunk uprooting (e.g., Schaller 1963; Casimir 1979; Fossey 1983; Carroll 1986; Mahaney Watts, and Hancock 1990; Nishihara and Kuroda 1991, Plumptre 1993; Remis 1993; Tutin and Parnell 1995; Breuer, Ndoundou-Hockemba, and Fishlock 2005; Wittiger and Sunderland-Groves 2007).

Zoogeomorphology embraces the biological sciences to explain how the interactions between animals and terrestrial systems guide the distribution of geomorphological processes and landscape formation. This contrasts with how geomorphologists historically have described landscape evolution. Instead, the physical sciences were used to explain how atmospheric and tectonic forces affect the distribution of local geomorphic processes and biota (Malanson, Butler, and Fagre 2007). Zoogeomorphology draws from three core concepts- bioprotection, bioerosion, and bioconstruction (Naylor 2005) to identify and quantify the interface of faunal induced spatio-temporal geomorphological change (Jones 2012). The discipline expresses incredible opportunity for interdisciplinary research. The results of this study are the product of bridging the expertise of primatology and physical anthropology with geomorphology.

Primate studies, although they do not explicitly define it as so, document various scales of zoogeomorphic activity among nonhuman primates. Wild chimpanzees (*Pan troglodytes schweinfurthii*) in Uganda have been observed using their hands to, "… dig holes ('wells') in sandy riverbeds [to obtain] drinking water" (McGrew, Marchant, and Hunt 2007, 241). Chacma baboons (*Papio ursinus*) in South Africa (SA) use their forefeet and fingers in sub-surface foraging for insects, roots, acacia seeds, and tubers (Hamilton, Buskirk, and Buskirk 1977). They, too, have been observed to engage in 'water-well digging' to the extent of permitting their head to enter cavities large and deep enough to reach the water table (Hamilton, Buskirk, and Buskirk 1977).

Gorilla spp. exert an exceptional degree of influence on their physical environments. Most notably, their role as keystone species in forest regeneration via endozoochory dispersal mechanisms has been well documented (Tutin et al. 1991, Voysey et al. 1999). However, their habitat use and ranging patterns elicit behavioral responses selected to extract certain resources, such as roots and sub-surface insects, by mechanically manipulating the physical surface in order to exploit them. George Schaller's (1963) 20-month longitudinal study on the ecology and behavior of mountain gorilla (*Gorilla beringei beringei)* populations in the Virunga Volcanoes revealed the earliest and most comprehensive observations of zoogeomorphic activity. Schaller (1963) recorded geophagy (soil eating) sites extending 15 feet (5m) long and 6 feet (2m) wide, and several bare-soil bottom nest site constructions on steep slopes. Within the same region, Dian Fossey (1983) documented a geophagy site so highly incised that a cavern developed large and deep enough to permit a single gorilla to enter and disappear into the chasm. In the Central African Republic (CAR), Carroll (1986) counted 96 termite mounds that had been dismantled by western lowland gorillas (*Gorilla gorilla gorilla*) in the interior savannah habitat of their home range during the wet season. These early cases reveal the direct influence gorillas have on the landscape and introduce opportunities for zoogeomorphic inquiry that include but are not limited to:

1. Spatio-temporal zoogeomorphic target site and habitat identification.
2. Pedological analysis of disturbed areas to determine changes in *in situ* morphology and chemical composition.
3. Quantitative and qualitative description of micro and macro topographic formation.
4. Analysis of the rate of landscape formation and decay of disturbed sites.
5. Identification of inter-intra specific zoogeomorphic activity.

6. Exploration of secondary biogeomorphic introductions that result from gorilla zoogeomorphic activity.
7. Field study to measure frequency and duration of zoogeomorphic behavior.

Currently, reports of gorilla zoogeomorphic activity are scattered throughout the literature of various disciplines and mostly functions as supplementary data to primary research goals (e.g. Cipolletta et al. 2007). Presently, there is no study that exclusively focuses on geomorphic implications of gorillas on the landscape. Although, Nishihara and Kuroda (1991) completed a year-long case study in which they documented soil scratching traces in the Ndoki forest of northern Congo. No geomorphic analysis was conducted; however, their research rides the threshold of geomorphological inquiry. Their results provided valuable insight into the seasonal extent of gorilla scratching behavior. Nevertheless, the complexity of gorilla social systems, behavioral ecology, and their phylogenetic relationship with human primates (*Homo sapiens*) continues to dominate research.

The purpose of this study is to explore gorilla behavior and habitat use through the lens of zoogeomorphology and to introduce zoogeomorphic exploration within gorilla research. To achieve this goal, specific objectives were to: (1) provide a qualitative description of documented cases of zoogeomorphic activity, (2) quantify literature reports, and (3) extrapolate potential trace specific geomorphic responses. A content analysis of literature found either in print or online within twenty-nine journals, four books, and seven organization webpages (Table 1) was exhaustively mined to capture the greatest extent of qualitative and quantitative data possible. Qualitative data (e.g. behavioral observations and photographs) extracted from the literature contributed 58 percent of the total data collected for this study, with quantitative data (e.g. dimensional measurements of excavated holes) making up 42 percent.

A conventional approach was adopted using the definition of zoogeomorphology as defined by Butler (1992) to guide the process of identifying and organizing cases of gorilla zoogeomorphic activity into nine meaningful categories. Descriptive statistical analysis was used to generate a quantitative description of each category of gorilla zoogeomorphic activity and overall summary of collected data.

The conceptual framework guiding this research hypothesizes that within their home ranges, gorillas function as zoogeomorphic agents. They are selectively forced to interact with the physical environment by mechanically modifying, sculpting, or maintaining it to exploit certain resources (e.g. sub-surface vegetation, minerals), meet diurnal requirements (e.g. day/night nest), or overcome landscape barriers (e.g. crossing swampy terrain). The physical signatures (e.g. holes, pits) left behind from their activity subsequently contribute to indirect geomorphic processes resulting from atmospheric (e.g. wind, precipitation) and other ecological forces (e.g. lateral root sprawl from nest deposited endozoochors). Figure 1 illustrates the conceptional framework for this study.

Early concepts in geomorphology developed by William D. Thornbury (1969) proposed that to understand and appreciate the origin of landforms, it is necessary to understand the "…processes in landform evolution" (Thornbury 1969, 21). Studies on the geomorphic responses of *Gorilla spp.* activity are necessary to refine our understanding of their role as bio-modifiers. Without this knowledge, vital pieces of information could be excluded in future conservation planning and habitat suitability modeling. This research is a step forward because it offers a theoretical standing for exploration of a gorilla's zoogeomorphic niche; laying the foundation for future field research. It expands on the repertoire of studied megafauna within Zoogeomorphology, therefore, contributing to the depth and breadth of the discipline. Finally, this study embraces the intellectual advantage of interdisciplinary research.

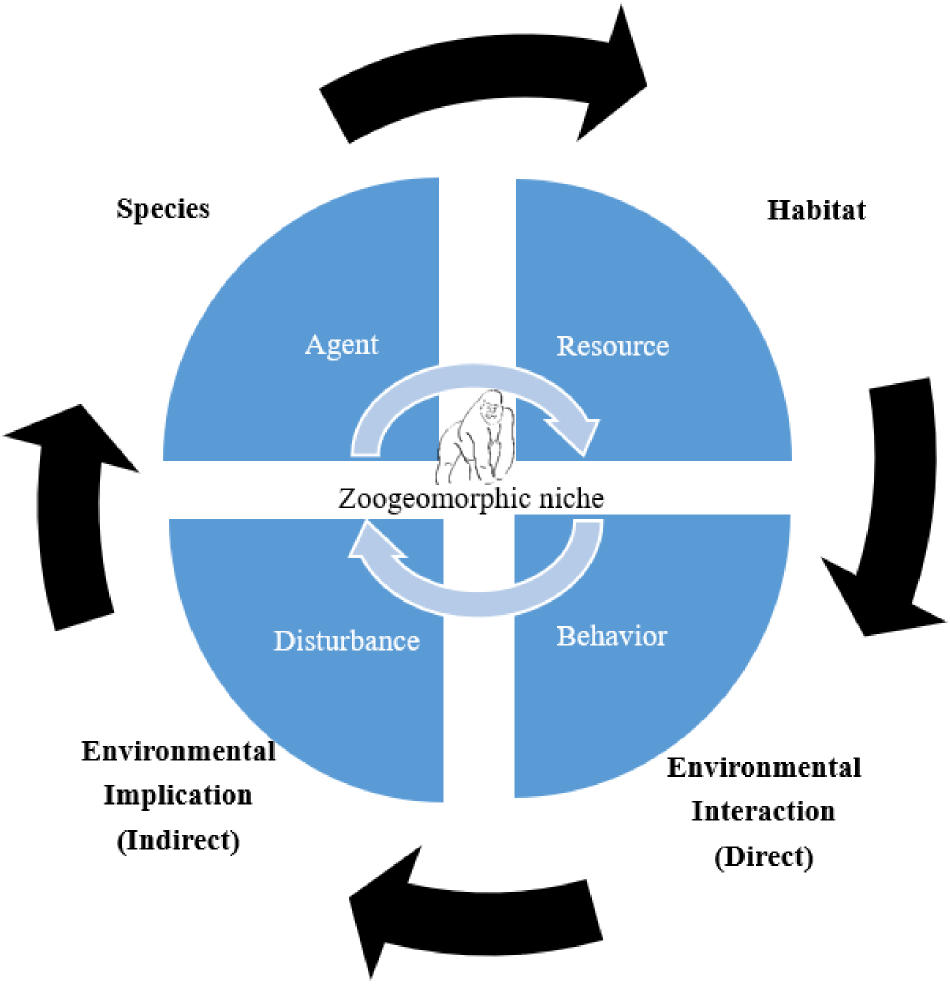

Figure 1. Conceptual model of gorillas as zoogeomorphic agents.

Table 1. Content Reviewed (1963-2016)

Journal	
African Journal of Ecology	Journal of Biogeography
American Journal of Physical Anthropology	Journal of Human Evolution
American Journal of Primatology	Journal of Mammalogy
Animal Behaviour	Journal of Primatology
Behavioural Processes	Journal of Tropical Ecology
Biodiversity and Conservation	Journal of Zoology
Biotechnology, Agronomy, Society and Environment	Nature
Ecological Applications	PloS Biology
Folia Primatol	PloS One
Folia Primatologica	Primate Conservation
Forest Ecology and Management	Primates
Internaltional Journal of Primatology	Stochastic Environmental Research & Risk Assessment
Journal of Applied Ecology	Tropics

Book	Organization
Gorilla Biology: A Multidisciplinary Perspective	Dian Fossey Gorilla Fund International
Gorillas In The Mist	International Union for Conservation of Nature and Natural Resources
Mountain Gorillas. Three Decades of Research at Karisoke	The Cross River Gorilla Conservation Program
The Mountain Gorilla. Ecology and Behavior	The Leakey Foundation
	World Wildlife Fund
	United States Fish and Wildlife Service
	World Resources Institute

II. LITERATURE REVIEW

Gorillas are the largest of the great apes (Hominidae) which also includes extinct and extant orangutans (genus *Pongo*), chimpanzees (*Pan*), and human beings (*Homo*) (Nichols 1993). Their populations are patchily distributed across east, central, and west Equatorial Africa (Figure 2) where they inhabit lowland and montane primary and secondary tropical forests. There are two species of gorilla, the western gorilla (*Gorilla gorilla*) that covers a geographic range of approximately 709,000 km^2 (273,746 mi^2) and the eastern gorilla (*Gorilla beringei*) that covers about 112,000 km^2 (43,243 mi^2) (Lang 2005). *G. gorilla* sub-species include the western lowland gorilla (*G.g. gorilla*) and the Cross-River gorilla (*G.g. diehli*). *G. beringei* sub-species include the mountain gorilla (*G.b. beringei*) and the eastern lowland gorilla (*G.b. graueri*). All species are listed as critically endangered (CR) by the International Union for Conservation of Nature and Natural Resources (IUCN) because of threats ranging from habitat loss and degradation to poaching and disease (Kormos et al. 2014). Currently, an estimated 200-300 *G. diehli* individuals persist in the lowland montane forests of Cameroon and Nigeria, making them the most vulnerable to extirpation from increasing anthropogenic pressures such as agriculture and poaching (World Wildlife Fund 2017) (Table 2).

Table 2. Gorilla classification and species description

Species	Sub-species	Distribution	Range (km^2/mi^2)	Habitat	Primary Diet	Protection (IUCN-Critically Endangered)
Western Gorilla (*Gorilla gorilla*)	Western lowland gorilla (*G.g. gorilla*)	Cameroon, Central African Republic, Equatorial Guinea, Gabon, Republic of the Congo (ROC), Angola, Dem. Rep. of the Congo	708,250 km^2/ 273,456mi^2	lowland, swamp, and montane forests	Frugivory	1. Dzanga-Sangha Special Reserve 2. Nouabale-Ndoki National Park 3. Lobeke National Park
	Cross River gorilla (*G.g. diehli*)	Nigeria, Cameroon	750 km^2/ 290mi^2	low-lying, sub-montane forests	Frugivory	1. Tofala Hill Wildlife Sanctuary (not yet confirmed)
Eastern Gorilla (*Gorilla beringei*)	Mountain gorilla (*G.b. beringei*)	Democratic Republic of the Congo, Uganda, Rwanda	92,300 km^2/ 35,637 mi^2	montane forests of the Virunga Volcanoes	Folivory	1. Bwindi Impenetrable National Park 2. Virunga National Park 3. Volcanoes National Park 4. Mgahinga National Park
	Eastern lowland gorilla (*G.b. graueri*)	Democratic Republic of the Congo	19,700km^2/ 7,606mi^2	primary and secondary in both highland and lowland forest	Folivory	1. Kahuzi-Biega National Park 2. Maiko National Park 3. Kisimba-Ikobo Nature Reserve 4. Tayna Nature Reserve 5. Usala Forest 6. Virunga National Park

Robbins, Sicotte, and Steward 2001; Walsh et al. 2003; Hopkin 2007; Plumptre et al. 2016; World Wildlife Fund 2017

Gorillas are diurnal and primarily terrestrial dwelling species that occasionally engage in arboreal activity. They mostly exhibit quadrupedal knuckle-walking locomotion with occasional bipedalism (Schaller 1963). On average, male gorillas weigh between 300 to 485 pounds (136-219 kg) with females weighing about half that. Standing, gorillas can reach heights between 4 to 6 feet (121-182 cm) (Leigh et al. 2003). They exhibit "… age-graded social structures with the existence of and transition between solitary individual and one-male, multimale, and all-male gorilla units" (Robbins 2001, 31). Groups are comprised of approximately two to fifty individuals (Schaller 1963). One silverback male dominates over several females, blackback subordinate males, juveniles, and infants. In cases where there is more than one silverback in a group, a linear hierarchy based on body size determines dominance (Schaller 1963). Intrasexual selection is preferentially reserved between the dominant silverback and all group females although sneak copulations between extra-group males and nulliparous females have been documented (Sicotte 2001). Gestation is approximately 259 days with an offspring produced every 3.5 to 4.5 years (Schaller 1963). Gorilla diet is dependent on habitat with *G. gorilla* exhibiting a primarily frugivorous diet (diet consisting of fruit) and *G. beringei* being mostly foliverous (diet consisting of the non-reproductive parts of plants). Overall, *Gorilla spp.* are described as omnivorous (diet consisting of non-reproductive parts of plants, fruit, and animals), however, they show a preference for herbaceous foods such as stems, pith, shoots, and leaves (Cipolletta et al. 2007). Seasonal geophagy (Mahaney 1993) and insectivory (Tutin and Fernandez 1983) have also been documented (Fossey 1983; Mahaney, Watts, and Hancock 1990; Mahaney, Aufreiter, and Hancock 1995).

Brief History of Zoogeomorphology

Biogeomorphology studies the two-way interactions between biotic and abiotic geomorphic systems (Viles et al., 2008). It straddles the disciplines of ecology and geomorphology in an attempt to establish ecological linkages with landscape formation and decay (Jones 2012). Although biogeography has received more attention within scientific literature, the concept was introduced in early studies by Charles Darwin and William Morris Davis (Butler and Sawyer 2012). Heather Viles brought the discipline back to life when she defined biogeomorphology as, “an approach to geomorphology which explicitly considers the role of organisms” (Viles 1988, 1). The ecologically-based theory of ecosystem engineering; referring to organisms that create, maintain, and modify habitat (Jones, Lawton, and Shachak 1994), emerged as geomorphologists were already making connections between faunal activity and landscape transformation (e.g. burrowing and digging). Butler and Sawyer (2012) noted the degree of parallelism between ecological and geomorphic studies of animals in landform surface processes (e.g. Cuddington et al. 2007; Renschler, Doyle, and Thoms 2007).

Emerging studies began bridging connections with biogeomorphology illustrating the research potential of interdisciplinary analysis. Naylor (2005) acknowledged the contributions of biogeomorphology to the field of geobiology by outlining three core processes: bioerosion, bioprotection, and bioconstruction. Bioerosion is concerned with the, “…weathering and/or removal of material by organic agency […] active or passive, mechanical and/or chemical erosion of the land surface by organic means” (Naylor 2005, 38). Ray et al. (2006) documented large scale movement of benthic substrate by pacific walrus (*Odobenus rosmarus divergens*) (~ 3 million tons). Conversely, bioprotection is the role of organisms that prevent or diminish earth surface processes such as that of erosion (Naylor 2005). Small communities of microorganisms, Naylor (2005) termed biofilms, function as direct and indirect forms of protection. However, through, "…active biological weathering" (40), biofilms can contribute to geomorphic erosional regimes. The trampling effects of animals and anthropogenic landscape disturbance cause substantial destruction of bioprotection mechanisms (Butler 2013). Finally, bioconstruction encompasses the materials (e.g. films, crusts, mounds, reefs) produced or developed by organisms (Naylor 2005). Autogenic ecosystem engineers, such as coral, are in this category. Murphy et al. (2016) introduced evidence of increased bioerosional rates of two Caribbean excavating sponge species (*Siphonodictyon brevitubulatum* and *Cliona tenuis*) on Grand Cayman coral reefs. Although bioerosion within reef systems is an important part of reef island sediment budgets (Murphy et al. 2016), loss of their bioconstruction frameworks results in significant changes to the "…physical structure of coastlines." (Knowlton 2001, 395).

Early studies conducted by Darwin and Davis explored the role of faunal activity on physical landscape processes (Butler and Sawyer 2012). Well into the 20th century, the discipline of geomorphology primarily focused on the geologic (Butler and Sawyer 2012) effects. With the resurrection of ecological systems within geomorphic analysis, Butler (1992) officially defined another sub-discipline of biogeomorphology-zoogeomorphology as the "…field of study which specifically examines animals as geomorphic agents" (179). Core concepts along with pioneer studies on the zoogeomorphic impacts of animals were outlined, and the concepts were greatly expanded in Butler's (1995) book *Zoogeomorphology- Animals as Geomorphic Agents*. There remains much to be explored on this subject and research continues to gain momentum, especially among female researchers (Engvall 2013). This study expands on the sub-discipline of zoogeomorphology with special attention given to *Gorilla spp.* as zoogeomorphic agents within protected areas in Equatorial Africa.

Trends in Primate Research

Existing physical and observational evidence of lithospheric disturbance by *Gorilla spp.* warrants further exploration of associated existing trace specific geomorphic responses. Cases of zoogeomorphic activity are documented within non-human primate research. However, the literature reveals two underlying trends: an (1) emphasis on phylogenetics, socio-behavioral/feeding ecology, and biology with limited zoogeomorphic data that supplements primary research goals; and (2) available data is mostly confined to nest site research. This is because of their relatively large size which makes nests easier to detect. Also, nest densities are high because gorillas construct both day and night nests.

Although Butler (1992) was the first to use the term, accounts of gorilla zoogeomorphic activity have been documented as early as the 1960s. George B. Schaller (1963) introduced photographic evidence of holes dug by *G. beringei*. He also collected quantitative data on terrestrial nest site constructions and offered detailed illustrations of their spatial arrangement. His work pioneered future *G. beringei* studies in the region and continues to make considerable contributions within primate research. Subsequent great ape research followed a similar suite and embraced field methodologies mostly restricted to focal observation techniques (e.g., Wittiger and Sunderland-Groves 2007), pedological analysis (e.g. Mahaney 1993), and limited quantitative data (e.g. Casimir 1979). Studies continue to fall short with documenting the subsequent geomorphic responses from landscape disturbance. Two decades following Schaller's (1963) work, Dian Fossey (1983) offered a brief account of mines created by seasonal gorilla "soil-eating binges on Visoke's ridges" (52), a phenomenon hypothesized because of the soil's high calcium and potassium content (Fossey 1983; Mahaney 1993). She observed the subsequent effect of the surrounding root architecture in adapting and eventually supporting the 'eaten' chasm- a form of phytogeomorphic activity. Fossey's work produced significant interest in *G. beringei* populations of the Virunga Mountains, currently making them one of the most studied gorilla species on the planet (World Wildlife Fund 2017). Today, Fossey's legacy endures after five decades of gorilla research at the Karisoke Research Center in Rwanda's Parc National des Volcans (Watts 1989; Mahaney, Watts, and Hancock 1990; Mahaney 1993, Krishnamani and Mahaney 2000). Within the same region, Plumptre (1993) focused on the trampling effects of *G. beringei* populations and documented the rate of regeneration of vegetation. His study revealed the extent of damage from trampling was, expectedly, determined by habitat type with *Senecio mariettae* (a flowering, semi-scandent shrub that reaches 2 to 10 meters high) being the most vulnerable to ranging gorillas.

Additional accounts of zoogeomorphic activity emerged in the 20th century but peripherally within the literature of other disciplines. Nishihara and Kuroda (1991) conducted the first detailed field study of *G. gorilla* soil-scratching behavior in the northern Congo. They analyzed the seasonal variability of soil-scratching traces in the Ndoki forest of northern Congo, hypothesized to be a result of sub-surface foraging for earthworms and insects in riverine *Gilbertiodendron* forests. The frequency of mound excavation was correlated with the wet season when mound casings softened from high precipitation regimes making them easier to excavate. Yamagiwa et al. (1991) took a single depth measurement (19cm) of a soil scratching trace found at an ant-feeding site on the slopes and ridges in the Itebero region of the DRC. Their brief description introduces research opportunities exploring the geomorphic effects of seasonal excavation habitats located in areas with variable relief.

Presently, 21st century research has focused its attention on gorilla nest sites because of their relative abundance and large size that makes them more easily identifiable than other signatures (Iwata and Ando 2007; Funwi-Gabga and Mateu 2012). Gorillas construct day and night nest sites that function for sleeping, resting, giving birth, mating, and dying (Willie et al. 2014). Construction type (e.g. arboreal or terrestrial, full or partially vegetated) and location (e.g. slope, flanking trees) varies with season and individual need. For example, during the peak wet season, gorillas may construct nest sites entirely of vegetation to insulate themselves from saturated surfaces or opt to construct arboreal nest sites.

The geomorphic significance of nest constructions is mostly represented in the subsequent indirect geomorphic processes that result from exposed soil nest cups. With respect to weight, wild gorillas exhibit extreme sexual dimorphism. Mature males weigh between 150 (68kg) and 500 (226kg) pounds (Schaller 1963) with females weighing half. Their body weight exerts significant localized pressure on nest site bottoms and could contribute to variable soil compaction. Sediment runoff and erosion are potentially some of the geomorphic implications of nest sites although no studies have yet to address them. The majority of research focuses on nest sites as proxies for census data and as mechanisms for seed recruitment (Rogers et al. 1998; Mehlman and Doran 2002; Iwata and Ando 2007).

The potential for zoogeomorphic research in nest site data lies in the scale of biogeomorphic (fauna and flora) activity. In consideration of the direct mechanical modifications of gorilla during the nest building process, changes to soil structure are actively occurring. These include soil displacement, mass movement, and pedoturbation (Platt et al. 2016). The introduction of secondary biogeomorphic agents are another area for zoogeomorphic inquiry. For example, seeds that successfully germinate in nest sites become mechanical bioturbators (Phillips and Marion 2006) as their roots begin to spread laterally, continuously mixing soil horizons. In addition, gorilla nest sites provide ideal conditions for small scale zoogeomorphic activity by dung dwelling insects. Petre et al. (2015) documented dung beetle activity following nest site abandonment and attributed it to deposited dung left behind. The burrowing and tunneling activity could be considered a form of micro-zoogeomorphology. Early studies on the influence of burrowing invertebrates (e.g., earthworms) have shown burrowing contributes to geomorphic processes such as soil creep and infiltration (Butler 2013). The combination of soil displacement, compaction, subsequent lateral root growth, and dung inhabiting species make gorilla nest sites exceptional hot spots for geomorphic analysis.

The knowledge that could be generated on the zoogeomorphic impacts of gorillas is far-reaching. Do *Gorilla spp.* contribute to landscape formation and decay? If they do, to what extent do they impact and initiate geomorphic processes? This study begins answering these questions and represents the first of its kind dedicated to examining existing data through the lens of zoogeomorphology.

III. RESEARCH METHODS

Site and Situation

The tropical humid climate in central Africa is determined by latitudinal position and the shifting Intertropical Convergence Zone (ITCZ). The distinct long wet season (September through June) brings heavy precipitation that exceeds ~80 inches (~2,000 mm) and affects the eastern coast, the Congo Basin, and to the western edge of the Rift Valley. The dry season (July through August) is brief with precipitation decreasing towards the east and west coasts and with increasing latitude from the Equator. Average annual temperatures range from 77 to 82˚F (25-28˚C). (Kayiranga et al. 2017). The tropical moist forests that dominate less than 50 percent of the region (Hall et al. 2004) are supported by heavy precipitation regimes. Vegetation is characterized by evergreen and deciduous mixed-species (e.g. *Piptadeniastrum africanum, Terminalia superba*) tropical lowland rainforest with marshy clearings and gallery forests (Mehlman and Doran 2002). A patchwork of primary forest and secondary forest accompany a mixture of dense and open herbaceous understory (Melletti et al. 2009) with scattered light gaps formed by ranging elephants (Carroll 1986). High altitude montane landscapes characterize the eastern portion of Equatorial Africa in the Virunga Volcanos. The area is recognized internationally and regionally for its high level of biodiversity and as one of the largest tracts of intact tropical forest on the planet. The Congo and Nile River are the two primary watersheds in the region. The Congo Basin drains an area of ~3.8 x 10^6 km^2 and contributes 50 percent of all annual freshwater discharge (~1300 km^3) from Africa to the Atlantic (Upstill-Goddard et al. 2017).

Gorillas are the largest living primates (Masi, Cipolletta, and Robbins 2009) with home ranges that span approximately 11 km^2 and often overlap with other gorilla groups (Bermejo 2004). Together, all four gorilla sub-species inhabit approximately 821,000 km^2 of habitat in central Africa (Figure 2) (Robbins, Sicotte, and Steward 2001; Walsh et al. 2003; Hopkin 2007, Plumptre et al. 2016; World Wildlife Fund 2017). The extent of their zoogeomorphic influence is potentially far-reaching considering their constant direct interaction with their physical environments. Habitat use and ranging behavior are primarily determined by nutritional requirements that vary spatio-temporally. The gorilla diet is comprised of 230 items and 180 species (Rogers et al. 2004). Harvesting of whole or parts of food resources selectively demands mechanical manipulation or modification of the physical landscape (Appendix E). Sub-surface vegetation of non-reproductive parts of plants (e.g. roots, tubers), soil dwelling insects (Appendix F), and minerals embedded in rock and soil (Appendix G) fall into this category. In addition, repeat visits to seasonal high-quality food patches (e.g. fruit, softened insect mounds) result in "…narrow, trampled trails" (Watts 1998, 683) from the reuse of a network of access paths created by multiple gorilla groups. The compounded impact of their weight and pressure distribution patterns (Matarazzo 2013) of knuckle-walking quadrupedal locomotion, make gorillas potential geomorphic agents of soil compaction.

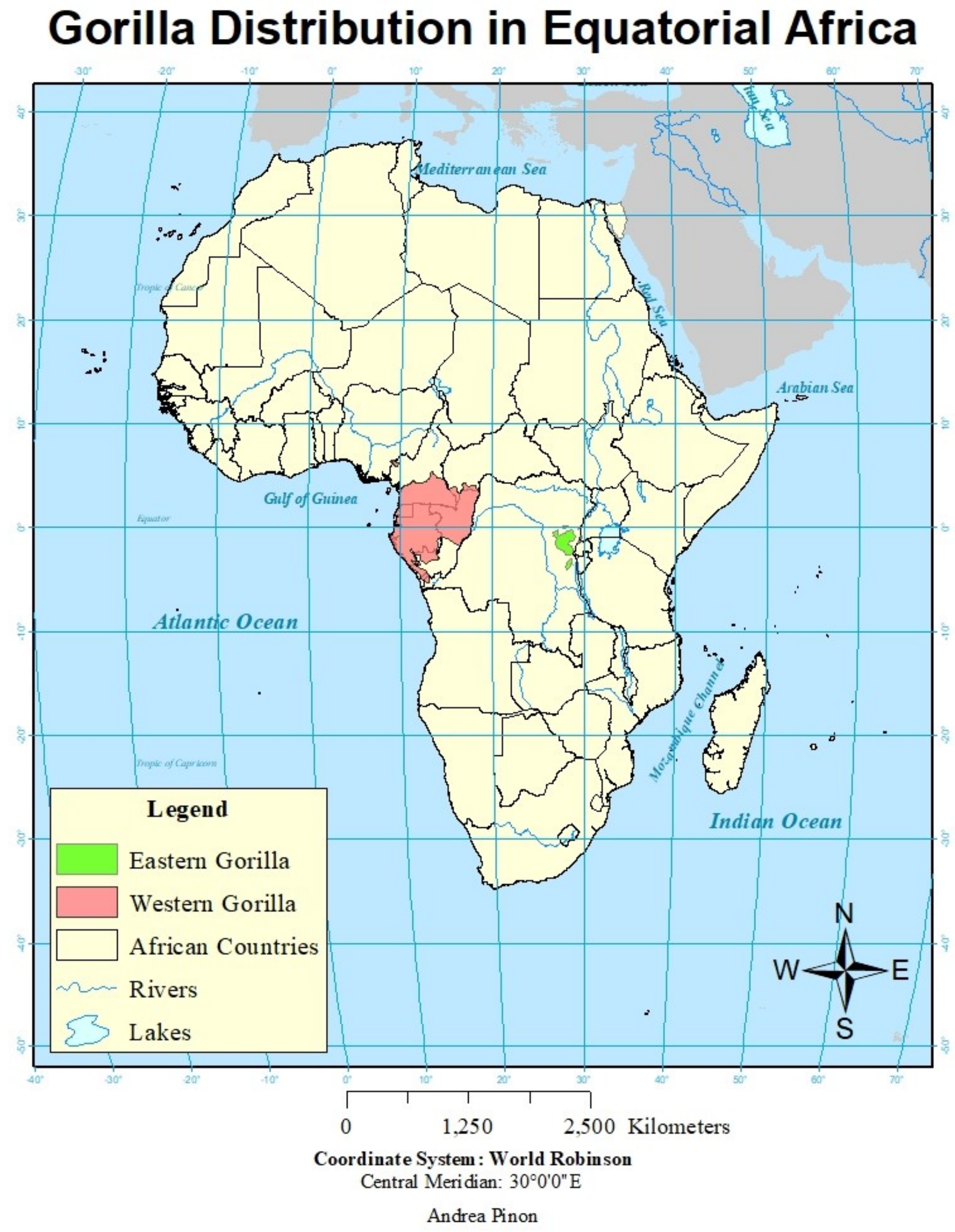

Figure 2. Gorilla distribution in Equatorial Africa (data source-World Wildlife Fund 2017)

Data

The majority of zoogeomorphic research uses data collected from field reconnaissance to assess the degree of geomorphic response of animals on the landscape and analyze the factors that influence geomorphological change. Current documented cases of gorilla landscape modification offer valuable insights into the behavioral-ecological context of zoogeomorphic activity, however, lacks focus on the geomorphic implications. For this research, a content analysis was used to generate data and provide qualitative and quantitative descriptions of gorilla zoogeomorphic activity. Results should be taken with caution as they are founded on the observations of other researchers. Extensive efforts were taken to gather as much data as possible to document all potential cases of gorilla landscape modification.

Content analysis

Content analysis techniques are designed to address study limitations associated with fragmented and scarce data. Content analysis is defined as a "research method for the subjective interpretation of the content of text data through the systematic classification process of coding and identifying themes or patterns" (Hsieh and Shannon 2005, 1278). It is primarily qualitative, however, statistical analysis (e.g. descriptive statistics) extends the depth of quantitative understanding of the research interest. Use of any one of the three distinct approaches to content analysis; conventional (inductive), directed (deductive), or summative; depends upon the theoretical framework, problem question, and purpose of the study (Hsieh and Shannon 2005). Within the constructs of this study, the conventional approach was the most appropriate method because it aims "…to describe a phenomenon […] when existing theory or research literature on a phenomenon is limited" (Hsieh and Shannon 2005, 1279). Contrary to more structured methods (e.g. directed approach), conventional analysis allows for inductive category development (Mayring 2000). Patterns and themes within the literature help to generate new insights of an existing theory (in this case, zoogeomorphology) and allow categories and sub-categories to "…flow from the data" (Hsieh and Shannon 2005, 1279). The model in Figure 3 illustrates the constructs of how data was organized and the nine categories of zoogeomorphic activity were determined.

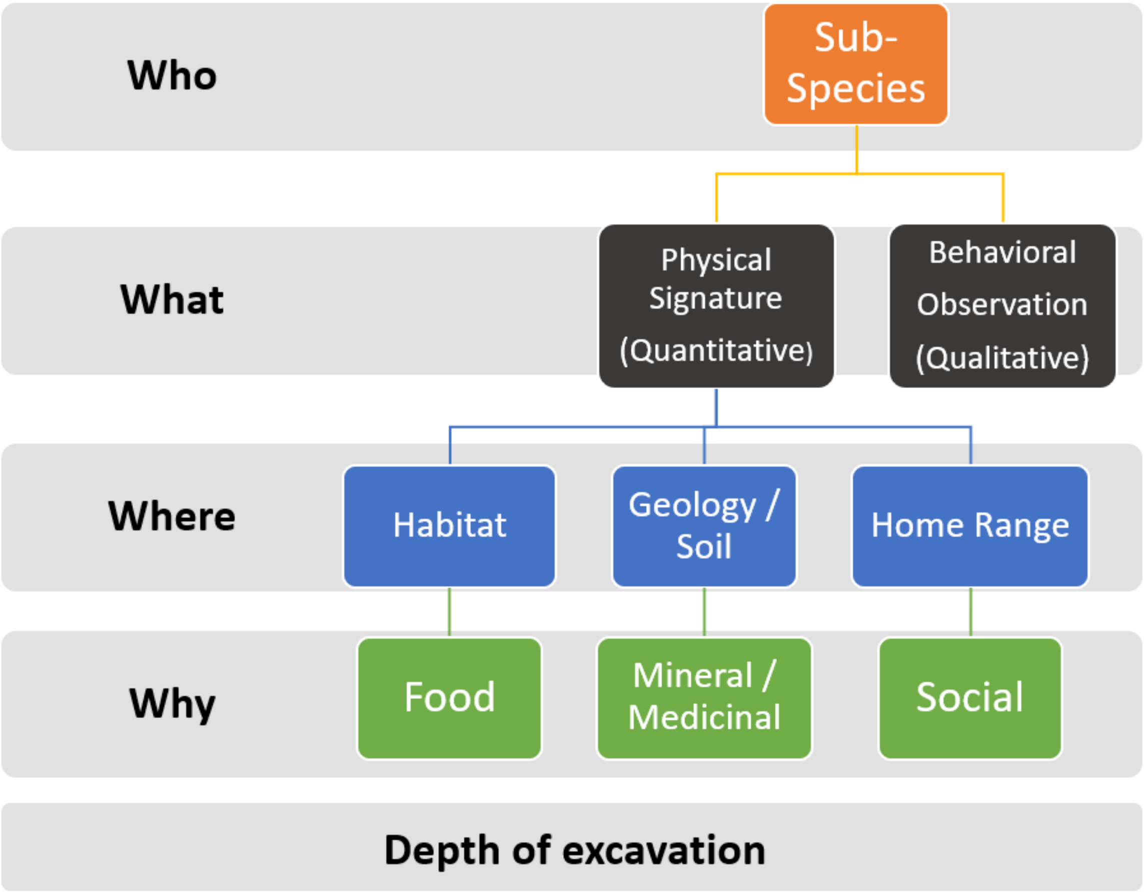

Figure 3. Model of content analysis framework for categorizing zoogeomorphic data.

Preliminary data

Raw data (Appendix C and D) was generated using printed and online literature published between 1963 and 2016 in twenty-nine journals, four books, and seven government and non-profit organization websites (Table 1). Google Scholar and the Texas State University Alkek Library Research databases were utilized to conduct online searches for peer-reviewed and full article publications. Key words such as, “gorilla and nest” or “gorilla and scratch” initiated the search, and subsequently, returned ‘author-supplied key terms’ and database ‘subject terms’ guided future searches. Therefore, it should be noted that journals listed in Table 1 were not initially selected for the literature review, rather, the list was generated from relevant articles collected for the content analysis. The purpose of initiating searches using key terms instead of journals was to mitigate the issue of fragmented data published in journals from multiple disciplines. The definition of zoogeomorphology served as a guide to identify themes and patterns. Nine categories of gorilla zoogeomorphic activity were identified (Table 3).

Table 3. Identified gorilla zoogeomorphic categories and their descriptions.

Category	Description
1. Soil scratching	Scratching of the forest floor with hands.
2. Soil scraping	Scratching of the forest floor with incisors.
3. Excavated chambers and depressions	Excavation of soil horizon greater than 13 cm (5 in).
4. Bare/semi-bare soil nest sites	Individual or group nests constructed entirely of soil or with soil exposed nest cup bottom and herbaceous rim.
5. Insect mound excavations	Mechanical dismantling of insect mounds.
6. Trampling	Soil compaction along frequently used individual and group feeding/ranging trails with clear reduction or complete loss of vegetation.
7. Hand/Knuckle and foot prints	Soil surface indentations of prints.
8. Tool use	Earth surface disturbance resulting from the use of detached object as a tool.
9. Trunk uprooting	Uprooting of shrub and tree trunks.

Collected data was separated into two excel spreadsheets, one for quantitative data and a second for qualitative data. They were then further organized into the nine categories (Table 3). It is important to note that not all categories were represented in both the qualitative and quantitative data sets (quantitative data = 8 categories represented, qualitative data = 9 categories represented). Statistical analysis (measures of central tendency and dispersion) was calculated for each variable assigned to each of the categories. Analysis was weighed against the total number of collected variables from the literature, the study region signature specific measurements (e.g. dimensions for all excavated holes), and sub-species. Sum and average values was also calculated for all variables obtained from the literature.

Qualitative data

Qualitative data included any direct observations of zoogeomorphic behavior (e.g. Watts 1989), frequency and duration of bouts (Cipolletta et al. 2007), identification of zoogeomorphic target areas (e.g. Williamson et al. 1990), any published photographs of physical traces (e.g. Nishihara and Kuroda 1991), and indirect evidence of earth surface disturbance (e.g Tutin and Fernandez 1983). Appendix B provides a summary of qualitative data collected. Information on target vegetation, geology, and insects relevant to zoogeomorphic activity was included in this data set.

Quantitative data

Quantitative data included any documented dimensional measurements (e.g. area or size of excavated hole) of physical traces found during study periods (e.g. Cipolletta et al. 2007). Discrete data was also included such as the number of excavated mounds counted and provided by the published author(s) (e.g. Carroll 1986).

Methods

This research used data collected with the use of a content analysis of non-human primate literature published online and in print between years 1963 to 2016. Data that captured the location, stimulus, behavior, and habitat associated with gorilla zoogeomorphic activity was recorded. Statistical analysis using Microsoft Excel 365 was used to explore trends in these data sets and zoogeomorphology literature used to draw conclusions from disparate data. Figure 4 is a flow chart of methods used to gather data sets, conduct analysis, and generate results for this research.

Study subjects

This paper only examines peer reviewed published studies on wild gorilla populations with no limitations on the length of the study period. All four sub-species of gorilla taxa were included with no preference given to the number of individuals or size of group observed. Subjects also included extinct and extant populations in protected regions of central Africa. This was to ensure data for this research is founded under the most pristine environmental conditions with little anthropogenic influence.

Descriptive statistical analysis

To uncover patterns and trends of zoogeomorphic data found in the literature, descriptive analysis was used to interpret aggregate data sets for both qualitative and quantitative variables. Data collected from the content analysis was organized into excel spreadsheets and measures of central tendency (mean, median, mode) and dispersion (standard deviation) were calculated using the functions tool in Microsoft Office 365 Excel. Descriptive information was determined for both the qualitative and quantitative data and for each category. If data provided in the literature was a range, the median was taken from that range (e.g. 13 cm-30 cm depth of excavated hole, median = 21.5) and that value used in the statistical analysis.

Extrapolating trace-specific zoogeomorphic response(s)

Key Zoogeomorphology and Biogeomorphology literature (e.g. Butler 1992, 1995) was used to hypothesize the geomorphic implications for each identified category. Notably, works from the Proceedings of the 42nd Binghamton Symposium in

Geomorphology (e.g. Butler 2012); Butler's 1995 book entitled, *Zoogeomorphology-Animals as Geomorphic Agents*, and articles recommended by Butler (e.g. Viles et al. 2008) were chosen for use in this research. The majority of published works in zoogeomorphology concentrates on micro and meso fauna with studies on megafauna largely limited. Also, invertebrates, ectothermic vertebrates, and mammals are currently represented in publications. For this study, megafauna were referenced when possible to maintain research homogeneity among mammalian species and also to fulfill a research need for studies on megafauna within zoogeomorphology.

Grizzly bear (*Ursus arctos horribilis*)

Grizzly bear studies (e.g. Butler 1992) were used when possible for comparison. *U. arctos horribilis* is relatively similar in size and weight. An adult can grow up to 3 feet (91 cm) with females weighing about 290 pounds (131 kg) and males, up to 600 pounds (272 kg). Although both species exhibit inter-specific differences in physical morphology, grizzly bear paws (28 cm width by 28 cm length) and gorilla hands (knuckle, 16.5 cm width by ~10.5 cm length) and feet (24-29 cm length) (Schaller 1963) are comparable in size. Combined with the weight of the species, they both exert exceptional mechanical influence on their physical environments. The physical signatures they leave on the landscape are also relatively similar. For example, grizzly bear dens (Butler 2012) were compared with gorilla nests (Casimir 1979). Finally, grizzly bears and gorillas have similar diets and therefore exhibit similar ranging and habitat use patterns. Their omnivorous diets require them to dig for sub-surface vegetation (e.g. roots, tubers) and for insects. Their large body sizes require that they also have large home ranges.

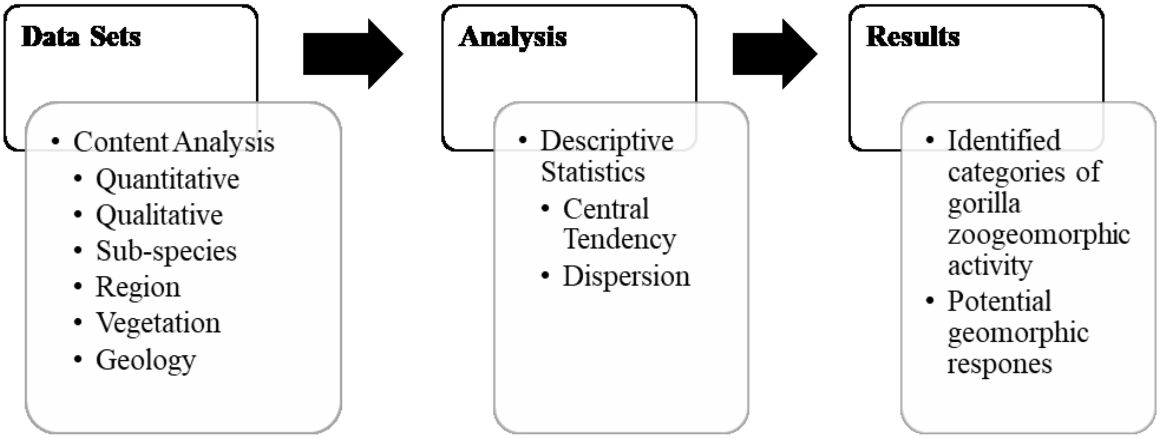

Figure 4. Flow chart of data sets, statistical analysis and results.

IV. RESULTS

Summary of aggregate data

This study employed the use of descriptive statistics to determine trends in available gorilla zoogeomorphic data found within published online and printed literature. The results of the analysis, for both quantitative and qualitative data, returned 106 total documented cases of zoogeomorphic activity. It was anticipated that quantified measurements would make up a small portion of zoogeomorphic information, however, this study reveals that there is almost an equal portion between the two types of data, disproving the former hypothesis. Discrete values encompassed most of the information collected with only eight instances where the author(s) provided data in the form of a range data set. These were concentrated in the quantitative information. All four sub-species of gorillas were represented in the qualitative documentation. The cross-river gorilla (*G. gorilla diehli*) was the only sub-species not represented in the quantitative measurements. A total of nine protected regions in Central Africa were represented in the content analysis (Table 4). However, not all regions were present for both qualitative and quantitative data (8 regions = qualitative, 9 regions = quantitative) For a full summary of analysis, see Appendix A and B. Appendix C and D provide all data collected from the literature. Some categories (e.g. soil scratching, trampling) were poorly represented in the literature and therefore no meaningful analysis could be conducted. This may be a confirmation of observing such behavior in the wild as a "…matter of serendipity" (Krishnamani and Mahaney 2000, 905) or an indication for the need for more focused research on these subjects.

The results presented in this thesis should be taken with caution as they are founded on the observations of other researchers. Study limitations include the lack of funding for field research and time to ground truth results. Extensive efforts were taken to gather as much data as possible and analysis conducted on the quantitative data available.

Table 4. Protected regions represented from content analysis

Protected region	
Collected qualitative data	Collected qauntitative data
Dzanga-Sangha Dense Forest Reserve, CAR (D-S.D.F.R.)	Dzanga-Sangha Dense Forest Reserve, CAR (D-S.D.F.R.)
Nouabalé-Ndoki National Park, ROC (N-N.N.P.)	Nouabalé-Ndoki National Park, ROC (N-N.N.P.)
Dzanga-Ndoki National Park, CAR (D-N.N.P.)	Dzanga-Ndoki National Park, CAR (D-N.N.P.)
Volcanoes National Park, DRC (V.N.P.)	Volcanoes National Park, DRC (V.N.P.)
Virunga National Park, DRC (Vi.N.P.)	Virunga National Park, DRC (Vi.N.P.)
Kahuzi-Biega National Park, DRC (K-B.N.P.)	Kahuzi - Biega National Park, DRC (K-B.N.P.)
Lope Reserve, Gabon (L.R.)	Lope Reserve, Gabon (L.R.)
Kagwene Gorilla Sanctuary, Cameroon (K.G.S.)	Moukalaba-Doudou National Park, Gabon (M-D.N.P.)
	Dja Biosphere Reserve, Cameroon (D.B.R.)

Zoogeomorphic activity

Soil scratching

Statistical analysis

Soil scratching is the mechanical manipulation of the physical surface using fingers and toes. The total number of times authors noted soil scratching activity was thirteen times. This is for both qualitative and quantitative data collection (Table 5). For this research, photographs (Figure 5), observed zoogeomorphic behavior, duration of bouts (in minutes), and indirect evidence (e.g. trails, feces samples) of soil scratching were organized as qualitative information. Nishihara and Kuroda (1991) and Cipolleta et al. (2007) were the only two articles that provided quantitative data for this study. Nishihara and Kuroda (1991) documented 465 soil scratching traces at an average frequency of 0.84 traces/km^2. The volume of displaced soil was not noted. Cipolleta et al. (2007) only provided the size of soil particles excavated after observing a scratching bout. Because of the discrete nature of these two observations, no statistical analysis could be used to detect trends. A list of this information is found in Appendix C. The frequency of qualitative data on gorilla soil scratching found in the literature totaled 10, making up 16 percent of all qualitative data collected for this study (see Appendix D). Author direct observations of gorillas engaging in soil scratching behavior made up the majority of data collected. A total of 5 instances where observations are documented in the literature was found. The aggregate value from these five, returned a total of 65 individual direct observations of gorillas engaging in soil scratching behavior (see Table 5). Studies by Mahaney et al. (1990) and Cipolletta et al. (2007) noted durations, in minutes, of soil scratching bouts. From the information provided in their published works, a conservative total of soil scratching bout duration was determined to last between 33-150 minutes. The amount of displaced soil resulting from soil scratching could not be found in the literature and therefore, no analysis could be performed. However, Cipolletta et al. (2007) noted the measurements of a "…hard particles" (466) which were documented to be ≤3 cm wide by 5 cm long. The authors did not note the number of particles they collected for these measurements.

Table 5. Soil scratching data

Summary of soil scratching data				
	Behavioral Observations	Bout Duration	Photographs	Indirect Evidence
Frequency of data collected from literature	5	2	1	2
Total Value	65 observations	33-150 minutes	2	9 feeding trails
Average	13 observation	61 minutes	-	-

Figure 5. Soil scratching trace near *G. dewevei* root (Nishihara and Kuroda 1991)

Geomorphic response

Very few studies document soil scratching by gorillas with only one study truly focused on the behavior (i.e. Nishihara and Kuroda 1991). This may be a matter of observational coincidence given the density of forest vegetation which limits vision to view the animals or that there may be a lack of interest to further study the subject. Soil scratching by wild mammals is documented within zoogeomorphology literature. This behavior is not to be confused with soil digging. For this research, these two have been separated into their own categories because of the difference in depth of soil excavation. Soil surface chambers and depressions that have been excavated in search of sub-surface vegetation will have a far greater local geomorphic impact than mere scratching of the surface. Although it may seem mediocre, soil scratching is still a form of faunalpedoturbation (the mixing of soil by animals) (Cavin and Butler 2015) that warrants further analysis to determine *in situ* changes such as in soil chemical and morphological properties.

Soil scratching has been documented among grizzly bears around the world. Their paws are armed with front claws that can reach approximately 10 centimeters in length (Butler 1992) and make impressive soil scratching tools. Butler (1992) noted that grizzlies rake the soil over their prey in an attempt to preserve the carcass for later consumption. Elgmork (1982) observed one of these debris piles and measured approximately 0.5 to 1.5 m^3 of soil that had been used to cover the carcass. Grizzlies are one of the few megafauna that engage in soil scratching behavior, however, most zoogeomorphic literature centers on mesofauna such as spiny anteaters (*Tachyglossus aculeatus*), Indian crested porcupine (*Hystrix indica*), and aardvarks (*Orycteropus after*).

Mitchell (1988) recorded single scrapes by *T. aculeatus* are 15-40 cm long, 12-25 cm wide, and 2-20 cm in depth (data taken from Butler 1995). *H. indica* scratches to depths of 10 cm when searching for food (Gutterman 1987). Like gorillas, *O. afer* consumes ants and termites, although insects make up a larger portion of their diet. Dean and Milton (1991) noted patchily distributed microtopographic soil scratching sites where *O. afer* searched for insects. They noted traces to be an average of 16 cm long, 8 cm wide, and 5-7 cm deep (data taken from Butler 1995).

Some of the geomorphic implications of soil scratching include elevated soil infiltration and erosion from the loosening of soil, thereby, "…increasing the soil's water retention capabilities" (Butler 1995, 65). It also leaves opportunities for dispersing propagules to deposit into these microtopographic pits. Seeds may then be able to germinate and contribute to phytoturbating (soil mixing by plants) of soil caused by lateral root sprawl (Phillips and Marion 2006). Scratching sites located on slopes and subjected to strong atmospheric conditions such as heavy precipitation and wind are liable to have increasing geomorphic influence. Dean and Milton (1991) estimated *O. afer* contributed a volume of approximately 640-900 cm^3 of eroded sediment from their many scratches located in termite mound habitats. Eldridge et al. (2012) recorded the small scratchings of heteromyid (mostly *Dipodomys* spp.) rodents in the semi-arid Australian woodlands. The total area of scratched soil was 1.8×10^{-4} m3. Their impacts led to changes in soil stability that varied with habitat and soil type. Nishihara and Kuroda (1991) documented 465 soil scratching traces at an average frequency of 0.84 traces/km^2. Given the geomorphic extent recorded among other animals, future research to expand on studies such as theirs is imperative to fully understand a gorilla's scratching influence on the physical landscape.

Soil scraping

Statistical analysis

Soil scraping is the mechanical manipulation of the physical surface using the incisors. The total number of times authors noted soil scraping activity was six times. This is for both qualitative and quantitative data collection (Table 6). The qualitative data that was found included direct observations of soil scraping behavior, identification of scraping sites, and any indirect evidence (e.g. soil smeared gorilla faces) collected. The quantitative data that was collected from the content analysis included the measurements for a single bare soil patch that had been scraped by gorillas (Schaller 1963). Descriptive statistical analysis revealed that qualitative data made up 83 percent of all soil scraping data and quantitative, 17 percent. An average of three cases (median=3, σ= 2) of scraping data could be found in the literature (Table 6). Soil scraping sites were the most documented with a total of 4 areas found. These were determined by identifying traces of incisors on soil surface (e.g. Schaller 1963). The extent of quantitative data obtained included one scraped soil patch measured by Schaller (1963) on the slopes of Mt. Mikeno in Volcanoes National Park, DRC (Appendix C). The area was 5 meters long by 2 meters wide. With no other data sets to compare this to, no statistical analysis could be conducted.

Table 6. Soil scraping data

		Summary of soil scraping data					
		Behavioral observations	Scraping sites	Indirect evidence	Grand Total	%	
Frequency of data collected from literature	Qualitative Data	1	3	1	5	83	Data collected from literature
	Quantitative Data	0	1	0	1	17	
Total Value		1 observation of gorilla scraping soil (geophagy)	4 scraping sites	1 gorilla group with soil smeared faces	6		
Average		1	2	1	3		
Median		1	2	1	3		
Standard deviation		0	1	0	2		

Geomorphic response

Animals that scrape the surface of the Earth, do so for a number of reasons. Porcupines "…gnaw and score rock outcrops in order to hone incisors" (Butler 1995, 96). The northern pocket gopher (e.g. *Thomomys talpoides*) use their teeth to claw the ground in search for food and to mark the beginnings of burrow construction (Zaitlin and Hayashi 2012). Other primates such as guereza monkeys (Oats 1978) and moustached tamarins (Heymann and Hartmann 1991) also scrape the surface with their teeth. The extent of geomorphic responses from soil scraping are diverse. Zaitlin and Hayashi (2012) noted the greatest influence of *T. talpoides* relates to soil structure and fauna and flora terrestrial communities. They recorded an increase in soil fertility and decreases in bulk density between the soil scraped mounds and surrounding soil. Although *T. talpoides* may be small, their densities and biogeographic preference for sloping ground make them exceptional geomorphic agents. The diversity of soil scraping studies within zoogeomorphology literature is mostly confined to burrowing vertebrates. However, there lies opportunities for research exploring soil movement resulting from surface gnawing by gorillas. Gorillas exhibit sexual dimorphism in their dental morphology. The mean length of a canine pair for *(G. gorilla gorilla*) adult male gorillas is 33.58 mm and for (*G. gorilla gorilla*) females, the mean length of a canine pair is 19.00 mm (Manning and Chamberlain 1994). The mean length of incisors for an (*G. beringei beringei*) adult gorilla is 10.8 mm and for (G. *beringei beringei*) females, the mean length of incisors is 10.9 mm (Booth 1971). These dental dimensions compounded with the jaw strength of these animals make gorillas masticating soil excavating machines. To appreciate the extent of subsequent geomorphic effects of soil scraping, more research is needed.

Excavated chambers and depressions

Statistical analysis

When gorillas excavate the earth, they leave significant physical impressions on the landscape that vary in size and shape. As expected, the descriptive statistical analysis confirmed that non-human primate literature offers little geomorphic data and, instead, tends towards data that focuses on the ecological implications of soil digging. A total of 17 cases ($\overline{x}$=9, σ=6) of zoogeomorphic activity was obtained from the content analysis. 76 percent (N= 13) were comprised of qualitative data with quantitative data making up 24 percent (N=4) of documented zoogeomorphic activity (Table 8). Qualitative information included author observations of excavating behavior, target sites, and any indirect evidence (e.g. Schaller 1963). Eight observations of soil displacement was documented in 4 articles (Appendix D). These include 4 instances of sub-surface foraging for roots and tubers (Figure 6) of plants (e.g. *Arundinaria alpine, Cynoglossum amplifolium*); 1 case of digging for ants (e.g. Watts 1989); 2 cases where gorillas tore at the ground to throw dirt and grass at researchers in a display behavior (e.g. Schaller 1963, Wittiger and Sunderland-Groves 2007); and 1 observation of gorillas engaging in geophagy at a mining site on Mt. Visoke in the Volcanoes National Park, Rwanda (Fossey 1983). One photograph of an excavated hole was documented in Schaller (1963). Seven geophagy mining sites were accounted for. Only two published works (Appendix C) collected quantitative data. Range data sets could only be obtained from the literature and to conduct the analysis, the median value of each data set was determined (see Table 7). Using the new values, the analysis determined gorillas excavate an average of 17 cm^3 of soil.

Table 7. Hole measurement data

Measurements of holes (in centimeters)		
	Recorded in Literature	Median Value
Width	13 - 25	19
Depth	13 - 30	21.5
Length	8 -15	11.5
Total		52 cm^3
Average		17.3 cm^3

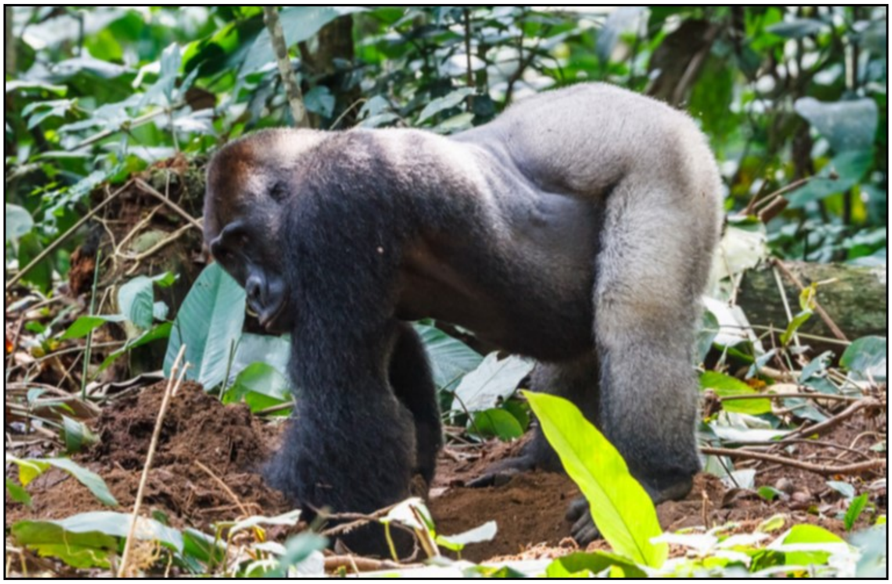

Figure 6. Gorilla digging for food (Ken Zaremba Photography 2014)

Table 8. Excavated chamber and depressions data

Summary of excavated chambers and depressions data							
		Behavioral observations	Excavating sites	Indirect evidence	Grand Total	%	
Frequency of data collected from literature	Qualitative Data	8	3	2	13	76	Data collected from literature
	Quantitative Data	0	4	0	4	24	
Total Value		8 observation of gorilla digging soil	7 geophagy mining sites	1 photograph, 1 area presumed digging	17		
Average		1	1	1	9		
Median		1	1	1	9		
Standard deviation		0	0	0	6		

Geomorphic response

Animals move soil by “pawing” (Butler 1995, 96) the earth. The extent of their influence is dependent on their target resource, the size and brute strength of the animal to move sediment, and their morphological mining tools (e.g. claws, hands, feet). Grizzly bears are unique zoogeomorphic agents in that they possess the best of all three characteristics. This research has demonstrated that gorillas show comparable influence to that of a grizzly bear and therefore, the geomorphic response of the two species is discussed.

Butler (1992) noted that grizzly bears seasonally dig for the bulbs of glacier lilies from April to November and contribute to patchily distributed areas of microtopographic pit and mound sites. He observed that although the excavations were shallow, they cover a large area. Gorilla show similar influences when they dig for roots and tubers. Schaller (1963) noted areas of numerous holes that had been dug for the roots of *Cynoglossum amplifolium* located in the Kabara Region in Volcanoes National Park, DRC. The geomorphic response of such excavations include soil churning, erosion of material downslope and eventual backfilling of holes from moving debris (Butler 1995). Also, deep depressions in the soil function as seed nursery sites, providing somewhat of a shelter for germinating propagules.

Bare/Semi-bare soil nest

Statistical analysis

Gorillas are diurnal and construct day and night nest sites that function for sleeping, resting, giving birth, mating, and dying (Willie et al. 2014). The content analysis revealed that approximately 66 percent (N=10) of the quantitative data found in the literature was allocated towards individual nest site research and 33 percent (N=5) for group nest sites. Quantitative information provided by authors consisted of the number of sites and nesting areas found and nest life span. A total of 2851 individual soil nest sites were accounted for between 1960 to 2016 with 379 group nesting areas where either all individuals in the group constructed a soil nest or at least one soil nest was found. An average of 285 individual soil nests were accounted for and 75 group nests. A minimum of 5 individual soil nests could be detected and a minimum of 24 group soil nests (Table 10). The content analysis revealed that 6 instances of recorded qualitative data was found in the literature (Table 9). This includes observations of gorillas constructing soil nest sites, photographs of nests, and an indirect evidence of nest sites (e.g. Schaller 1963). A total of three observations of soil nest constructing behavior was recorded. 1 photograph was taken by Schaller (1963), and Tutin and Parnell (1995) noted a couple of gorillas that had moved from an arboreal nest to a soil nest site located under a large "…roof of stout woody vines at a height of 50 cm" (70). Figure 7 was obtained after the content analysis; however, it reveals the extent of excavated soil used for nest site construction. Schaller (1963) recorded 3 cases of indirect evidence of soil nest constructions. He observed one abandoned nest site where the rim had been constructed of herbaceous vegetation with the soil nest cup left exposed. He could not confirm the age of the nest.

Figure 7. Mountain gorilla resting in soil nest site (Plataforma SINC 2016)

Table 9. Qualitative soil nest data

	Data Type		
	Direct Behavioral Observations	Photographs	Indirect Evidence
Total data sets collected	3	1	2
Value	-	1	2 soil nest sites

Table 10. Quantitative soil nest data

	Total	Average (N)	Median (N)	Standard Deviation	Minimum	Maximum
Individual nest site	2851	285.1	73	512.6	5	1739
Group nest site	379	75.8	74	33.9	24	119

	Frequency of Nest Site Recorded in Literature	Total
Individual nest sites	10	15
Group nest sites	5	

	Nest Site Lifespan (in days)		
	Recorded in Literature (Average)	Total	Average
Bare soil nest	4.3	23.4	11.7
Semi-bare soil nest	19.1		

Geomorphic response

Gorilla nest site constructions are among the most studied within non-human primate research. They are used primarily in census and survey studies because of their size and densities that make them more easily identifiable in the wild than other physical signatures. Field methods for identifying gorilla nest sites are often contested within the literature because of their similarity to sympatric chimpanzees (*Pan troglodytes*). However, the extent of research that exists and their obvious morphological significance, warrants these constructions as some of the most influential zoogeomorphic signatures. Moreover, a gorilla's decisions to construct their nest sites on mountain slopes (flat – 40˚) increases the degree of their geomorphic response (Appendix H).

Grizzly bears do not build nests; however, they excavate dens that compare in size. These excavations are not on the surface of the earth but are found below the ground as a means for thermal regulation and comfort (Butler 1992). Butler (1992) noted that these sub-surface cavities are typically made on slopes averaging 28-35˚. Similar to large gorilla nests, their geomorphic contribution leads to variabilities in ground instability and become susceptible to erosion and backfilling feedback loops of moving sediment. Butler (1992) estimated 2.6 m^3 of earth is displaced from grizzly chambers. Documentation of the size of nests and the amount of soil that is displaced warrants further exploration of their geomorphic influence (Figure 6). Unlike grizzly dens, gorilla nests present opportunities for seed nursery sites (Rogers et al. 1998) for a couple of reasons. First, the depth of the nest cup could potentially provide protection from ranging elephants, seed predators or the disturbing factors of aeolian and precipitation forces. Second, deposited gorilla feces provide seedlings with nutrient dense organic compost matter. Finally, gorilla nest sites potentially could introduce secondary zoogeomorphic forces in the form of burrowing insects. Nest sites affect dung beetle assemblage (Petre et al. 2015) because of the deposited feces left in in nest cups. Burrowing insects aid in seed deposition (Petre et al. 2015) while churning soil potentially contributing to *in situ* physical and chemical soil changes. Gorilla nest sites offer immense opportunities for further research within zoogeomorphology. They would be the most practical to begin field research for the reasons stated early. However, there are many more avenues of geomorphic analysis that could be taken to expand on their ecological roles as earth movers.

Excavated insect mound

Statistical analysis

Insect mound excavation is a patchily distributed and seasonal behavior of gorillas that is a result of their search for ants and termites to consume (Figure 8). The results of the content analysis revealed that mound excavation made up a significant portion of both the qualitative and quantitative data collected from the literature (see Appendix A and B). A total of 7 cases of documented quantitative mound data was obtained from 3 articles (see Appendix C), making up 16 percent of all zoogeomorphic activity collected. A total of 16 cases of qualitative mound data was obtained from 2 articles (Table 11), making up 26 percent of all zoogeomorphic activity collected. Observations of mound disassembly, timed bouts (in minutes), and number of visits to mounds was considered as qualitative data. Direct observations of gorillas dismantling mounds was most documented with 540 total observations. The descriptive statistical analysis returned an average of 90 observations of activity between the years 1989 to 2007. Six cases of measured bout activity were obtained from the content analysis with an approximate calculated total of 150 minutes of mound excavation activity. From the statistical analysis, gorillas on average spent 25 minutes breaking apart mounds (mostly termitaria, Cipolletta et al. 2007). Four cases where gorillas visited mounds were documented. The statistical analysis revealed an approximate total of 446 ($\bar{x}$=111) visits to mounds that were either located on the base of tree trunks, were located underground or were free standing mounds.

Table 11. Qualitative mound excavation data

	Data Type		
	Direct Behavioral Observations	Excavating bout	Mound Visits
Total data sets collected	6	6	4
Total	540 observations	150 minutes	446 visits
Average	90 observations	25 minutes	111 visits

Figure 8. Gorilla breaking apart termite mound (Dissolve 2018)

Geomorphic response

Insects make up a small portion of the gorilla diet (Cipolletta et al. 2007), however, they do exert a geomorphic impact on insect mound habitats. Africa has the richest diversity of termites in the world, housing more than 1000 species (Huis 2017). The variability in their mound construction influences the degree of gorilla excavation required to extract the insects. For example, *Macrotermes* spp mounds can reach heights of up to 5 meters high and 12 meters across (Huis 2017). Some are built against trees, have extensive networks below the earth's surface, or are free standing. The habitat they are located in also influences the geomorphic response of dismantling. Insects excavated in riparian or swampy areas may be subjected to high rates of erosion. Only a few dismantling techniques have been identified. Cipolletta et al. (2007) noted a 'pound-on-hand' technique where gorilla first took pieces off the mound then dismantled the soil portion in its hand to reveal the insects. Cipolletta et al. (2007) also noted gorillas use their brute force to destroy mounds in single blows. This is usually done when mounds casing softens making it easier to dismantle (Nishihara and Kuroda 1991). Grizzly bears also excavate insects; however, they predominately scratch and paw at the surface in search of worms and ants (Butler 1995). Their geomorphic effect, like, the gorilla is local changes in physical morphology of the soil surface where soil erodes and mixes with surrounding substrate.

Trampling

Statistical analysis

Trampling occurs when frequently used areas or trails lead to a visible detection of degraded or complete loss of vegetation than adjacent areas. The results of the content analysis revealed a greater portion of quantitative data available than qualitative data (see Appendix A and B). Table 12 below is the extent of qualitative data that was collected from three articles with eastern gorillas represented. Quantiative data (Table 13) provides insight into the area and distance of trampled habitat by gorillas. It should be noted that these trails may also have been used by other animals contributing to the effects. Gorillas exhibited the greatest trampling effects in bamboo habitats at a total of 15 m^2. This is expected since this is a prime food source. The statistical analysis revealed, gorillas trample an average of 7.5 m^2 which can vary by the size of groups and number of solitary individuals (Plumptre 1993). Feeding trails were organized into the quantitative data. Authors noted feeding and access trails between two different ant sites and trails located between a single ant site and 'other' sites. The statistical analysis revealed gorillas travel an average of distance of 168 meters on feeding trails, with trails between ant sites and 'other' sites the most widely used (N=236).

Table 12. Qualitative trampling data

Trampling qualitative data					
Gorilla beringei beringei		*Gorilla beringei graueri*			
1.5	13	1	5	10	13
Days gorillas spent in bamboo or woodland habitat.	Individuals in one gorilla group caused 15 square meter area of trampling	Gorilla group trail between ant-feeding sites	Solitary gorilla trails between 2 separate ant-feeding sites	Gorilla group trails between ant-feeding site and "other" site	Solitary gorilla trails between ant-feeding site and "other" site

Geomorphic response

Trampling is well documented in zoogeomorphology literature. Butler (1995) noted the erosional effects of trampling especially along streams and other inundated areas. Paws (e.g. *U. horribilis*), hooves (e.g. *Oreamnos americanus*), and feet (e.g. *G. gorilla*) alter plant communities by compacting the soil and influencing infiltration rates. The transfer of deposition of sediment that clings onto animals as they walk about the surface, incises and widens highly used trails. These impacts exhibit positive feedback loops when surface overland flow further erodes the soil. Butler (1995) also noted the chemical changes in trampled areas and attributed it to deposited fecal matter that enriches soil along animal trails. Butler (2012) photographed the erosional effects of mountain goats *(O. americanus*) in the Goat Lick avalanche path in Glacier National Park, Montana. Trampling and overgrazing of these steep slopes led to extreme loss of vegetation and greater frequency of debris flows. From the data, gorillas obviously contribute to trampling in their home ranges. The tropical climate and characteristic high precipitation regimes could potentially exacerbate their effects.

Table 13. Quantitative trampling data

Trampled Area (in square meters)				
Area	Total	Stimulus	Location	Additional Information
Bamboo habitat	10	Ranging	Parc Natonal des Volcans, DRC	Evidence of trampling in bamboo habitat caused by ranging of single gorilla group comprised of 13 individuals.
Saddle region	5	Ranging	Parc Natonal des Volcans, DRC	Evidence of trampling in saddle region located between Mt. Visoke and Mt. Karisimba. Caused by ranging of single gorilla group comprised of 13 individuals.
Total	Average	Median		Standard Deviation
15	7.5	7.5		2.5

Feeding Trail - Distance Between Sites (in meters)				
	Group		Solitary Male	
Trail	Recorded in Literature (Average)	Median	Recorded in Literature (Average)	Median
Ant Site - Ant Site	101	168.5	136	179
Ant Site - Other Site	236	337	222	358
Total				
Average		168.5		179

Hand/knuckle and foot prints

Statistical analysis

Gorillas leave noticeable tracks as they roam about their home ranges. They are primarily terrestrial dwelling species that occasionally engage in arboreal activity. They mostly exhibit quadrupedal knuckle-walking locomotion with occasional bipedalism (Schaller 1963). The content analysis revealed a greater portion of quantitative data available, making up 13 percent (N=6) of total zoogeomorphic activity collected from the literature. Qualitative data made up 5 percent (N=3) of total data recovered from the content analysis (Table 14). The statistical analysis returned a total of 465 total tracks that could be accounted for in the literature and 54 trails with clear foot and knuckle prints. These datasets were gathered from three different sources (see Appendix D) and no other data sets could be used to conduct an analysis. Measured dimensions of foot and knuckle prints provided by Schaller (1963) made up all quantitative information collected (Table 15). The statistical analysis returned the average width of a gorilla knuckle print to be 13 cm. The average length of foot prints was determined to be between 25 and 29 cm long. This is dependent on whether the toes are curled under the sole of the foot or extended.

Table 14. Qualitative hand/knuckle and foot print data

Hand/Knuckle and Foot Prints		
Gorilla gorilla gorilla		*Gorilla beringei beringei*
54	13	465
Observed gorilla trails with clear foot or knuckle prints	Days documented knuckle prints	Observations of hand or footprints

Table 15. Quantitative hand/knuckle and foot print data

Collected foot and knuckle prints (in centimeters)						
	Knuckle		Foot			
	Recorded in Literature	Median Width	Recorded in Literature		Median Length	
			Toes Curled	Toes Extended	Toes Curled	Toes Extened
Silverback	14.5 - 16.4	15.45	24 - 26.5	29	25.3	29
Blackback	13.5	13.5	No data	No data	No data	No data
Female	12 -14	13	No data	No data	No data	No data
Juvenile	9.5	9.5	No data	No data	No data	No data
Total		51.5			25.3	29
Average		12.9			25.3	29

Geomorphic response

The morphological significance of gorilla hands and feet make them potential geomorphic specialists. Compared with other zoogeomorphic agents, gorillas possess specialized fine and gross motor skills associated with hands and feet. Other species, such as the grizzly bear, are equipped with large paws and long claws that do not allow for extended mobility. This is not to argue that they lack or possess greater or lesser geomorphic influence. Rather, that gorillas have unique physical traits and motor skills that translate into distinctive signatures on the landscape. Butler (1992) described grizzly bears as "…formidable digging machines" (180) in part because of their 10 cm claws with which they dig into the soil. Gorillas, however, have fingers and toes which make them excellent diggers as well (Figure 9). The geomorphic significance of their tracks is the degree of surface area that they cover and their contribution to the effects of trampling and the transportation of sediment. As they move about their home ranges, and especially in areas of muddy terrain, soil that is sucked beneath their feet and paws moves with the animal and is deposited in other areas where it mixes with other soils. The weight of gorillas and grizzly bears exert variable degrees of compaction on the surface lending to more or less pronounced track prints. Also, as previously stated in the trampling section of these results, as feces are deposited with the ranging animal, they are compacted into the soil by the foot and paw prints of straggling animals.

A. B.

Figure 9. Bear track (A) and gorilla track (B) (Butler 1992 and Dewilde 2011)

Tool use

Statistical analysis

The extent of zoogeomorphic data on tool use was scarce in the literature. The content analysis returned only qualitative data (see Appendix D). Only one observation of potential zoogeomorphic disturbance was gathered. No meaningful analysis could be conducted for this category.

Geomorphic response

It is rare to observe tool use by wild gorillas. In fact, only two cases have been documented (e.g. Breuer, Ndoundou-Hockemba, and Fishlock 2005). Historically, the definition of tool use among non-human primates has undergone multiple revisions. The most influential definition is by Beck (1980) which states that tool use is “the external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself when the user holds or carries the tool during or just prior to use and is responsible for the proper and effective orientation of the tool” (10). Breuer, Ndoundou-Hockemba, and Fishlock (2005) observed a female gorilla that used a stick she had detached as a probing and postural support tool as she crossed swampy terrain (Figure 10). This category was included because of the turbating effects of the stick she uses and her wading in the water. Bison that wade across rivers in Yellowstone National Park, Wyoming, exert similar influence. This type of geomorphic response is difficult to quantify; however, it is obvious they impact the soil bottoms of inundated clearings.

Figure 10. Gorilla prods swampy substrate with stick (Breuer, Ndoundou-Hockemba, and Fishlock 2005)

Trunk uprooting

Statistical analysis

Only two cases of trunk uprooting from two published articles were obtained from the content analysis (Appendix D). No quantitative data was gathered and therefore no statistical analysis could be conducted.

Geomorphic response

For this research, trunk uprooting is the mechanical displacement of large shrubs (e.g. *Vernonia adolfi-fredericii*) or small trees. This type of physical signature is characteristic of microtopographic pit and mound landforms that are susceptible to erosion and local soil mixing between horizons. This is a rare behavior among wild gorillas, however, from a zoogeomorphic perspective is significant because of the variable degrees of surface disturbance that results. Pawlik (2013) described the influences uprooted trees have on the "…structure and layering of slope covers" (256). He noted the destabilizing effects of pit-and-mound topography on local surfaces and how they can contribute to movement of soil initiating erosional positive feedback loops. Breuer, Ndoundou-Hockemba, and Fishlock (2005) observed a female uproot a small tree trunk (1.3 cm long and 5 cm thick) at the edge of a swampy clearing. She used the trunk with one hand to stabilize herself while she dredged aquatic herbs towards her with the other arm (Figure 11). Picture A shows the intact tree trunk right before the female gorilla detaches it (Picture B) to use it as a tool (Picture C).

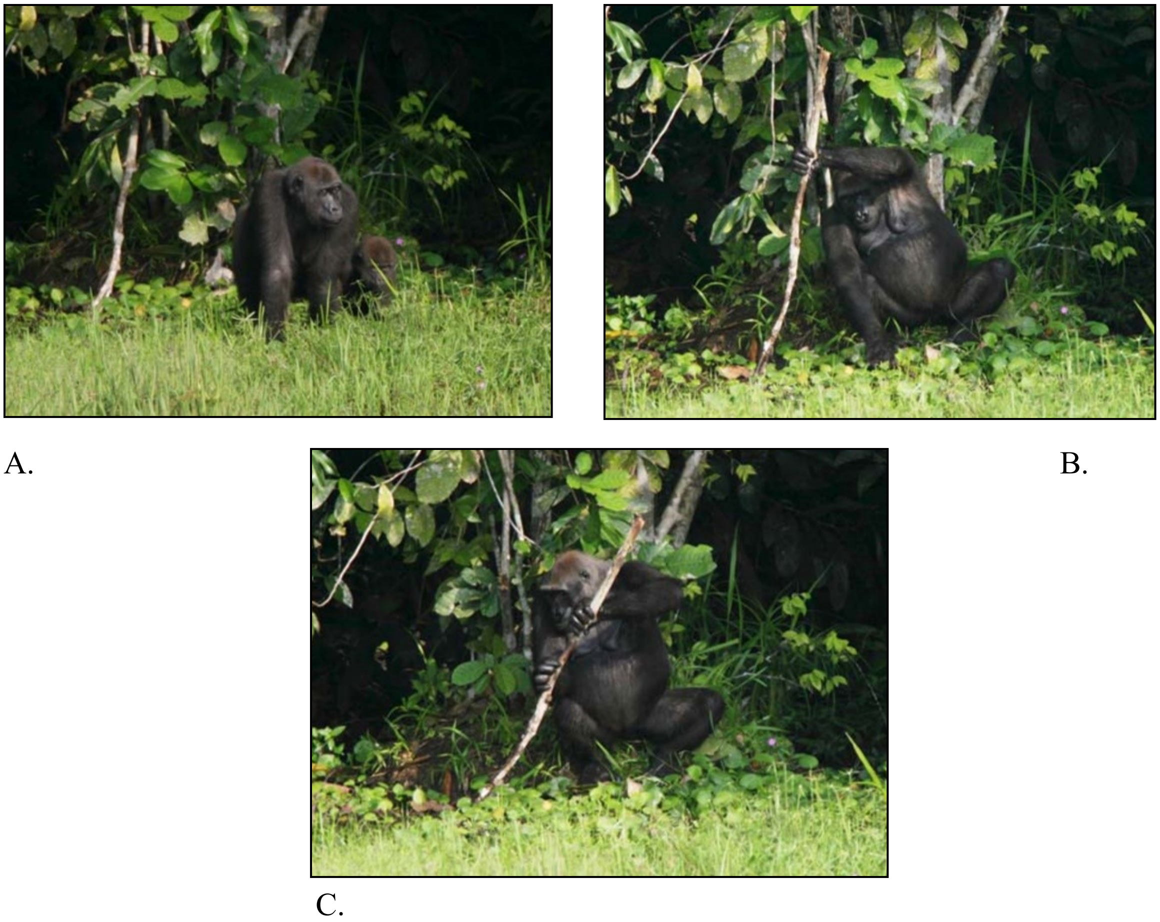

Figure 11. Gorilla detaching tree trunk (Breuer, Ndoundou-Hockemba, and Fishlock 2005)

VI. CONCLUSION

This thesis demonstrates the potential of gorillas as zoogeomorphic agents by highlighting cases of documented zoogeomorphic behavior found in non-human primate literature. This study identified nine categories of gorilla zoogeomorphic activity which include (1) soil scratching (with hands) and (2) scraping (with incisors) of the forest floor; (3) chambers and depressions created from surface excavation; (4) bare and semi-bare soil nest site constructions; (5) insect mound excavation; (6) trampling; (7) hand/knuckle and foot prints; (8) surface disturbance as a result of tool use; and, finally, (9) trunk uprooting. Indeed, gorillas can be considered significant zoogeomorphic agents because of the variety of categories of activities they employ and the amount of sediment moved as described in the limited quantitative studies.

Gorillas are a charismatic species, capturing the attention of researchers around the world. Current studies on these increasingly threatened species have made substantial contributions to their protection and conservation of their habitats. Lacking is research exploring the role of gorillas in sculpting, modifying, maintaining, and manipulating the Earth's surface. This thesis set the foundation for their role as biomodifiers by identifying nine categories of gorilla zoogeomorphic activity. Also, it attempted to quantify and describe the extent of their zoogeomorphic influence by referencing key zoogeomorphology studies of other fauna. The results presented are intended to lay the grounds for future field study and invite new research insights into one of the most well-explored species on the planet.

APPENDIX SECTION

APPENDIX A. Summary of quantitative data

Observations Collected Per Category

	Category						
	Foot & Knuckle Prints	Soil Nest Sites	Trampling	Chambers & Depressions	Scratching Traces	Scraping Traces	Excavated Mounds
Total Number of Observations	6	18	6	4	3	1	7
Percentage (total number of collected observations)	13	40	13	9	2	7	16

Observations Collected Per Protected Area

	Dzanga-Ndoki National Park, CAR	Virunga National Park - Kisoro region, DRC	Kahuzi - Biega National Park - Itebero region, DRC	Dja Biosphere Reserve, Cameroon	Nouabalé-Ndoki National Park, ROC
Total Number of Observations	10	2	2	1	3
Percentage (total number of collected observations)	23	4	4	2	7

APPENDIX A. Continued

Observations Collected Per Protected Area

	Dzanga-Sangha Dense Forest Reserve, CAR	Lope Reserve, Gabon	Moukalaba-Doudou National Park, Gabon	Volcanoes National Park - Mt. Mikeno, DRC
Total Number of Observations	6	3	1	17
Percentage (total number of collected observations)	13	7	2	38

Observations Collected Per Sub-Species

	Gorilla gorilla gorilla	*Gorilla gorilla diehli*	*Gorilla beringei beringei*	*Gorilla beringei graueri*
Total Number of Observations	24	0	16	5
Percentage (total number of collected observations)	53	0	36	11

Qualitative Observations Overall Summary

Total Number of Range Data Sets	8
Total of Non-Range Data Sets	37
Total Number of Collected Observations from Literature	45
Average Number of Collected Observations from Literature	6.4

APPENDIX B. Summary of qualitative data

Overall Summary

	Observations Collected	Study Regions Included	Zoogeomorphic Categories Included	Sub-Species Included
Total	61	8	9	4
Average	7	2	-	2

Collected Observations Per Zoogeomorphic Category

	Soil Scratching	Soil Scraping	Excavated Chambers & Depressions	Bare / Semi - Bare Soil Nest	Hand / Knuckle & Foot Prints	Excavated Insect Mound	Tool Use	Trunk Uprooting	Trampling
Total	10	5	13	5	3	16	1	2	6
% (Total Observations Collected)	16	8	22	8	5	26	2	3	10

Variables Collected Per Region Per Zoogeomorphic Category

Region	Soil Scratching	Soil Scraping	Excavated Chambers & Depressions	Bare / Semi - Bare Soil Nest	Hand / Knuckle & Foot Prints	Excavated Insect Mound	Tool Use	Trunk Uprooting	Trampling	Grand Total	%
D-S. D.F.R.	1	-	-	-	-	-	-	-	-	1	2
N-N.N.P	3	-	-	-	1	-	1	1	-	6	9
D-N.N.P.	3	-	-	-	1	8	-	-	-	12	20
V.N.P	1	5	10	4	-	8	-	1	6	35	57
K-B.N.P.	2	-	-	-	-	-	-	-	-	2	3
Vi.N.P.	-	-	1	-	-	-	-	-	-	1	2
L.R.	-	-	1	1	1	-	-	-	-	3	5
K.G.S.	-	-	1	-	-	-	-	-	-	1	2

APPENDIX B. Continued

Variables Collected Per Sub-Species Per Zoogeomorphic Category

	Category										
Species	Soil Scratching	Soil Scraping	Excavated Chambers & Depressions	Bare / Semi - Bare Soil Nest	Hand / Knuckle & Foot Prints	Excavated Insect Mound	Tool Use	Trunk Uprooting	Trampling	Grand Total	%
Gorilla gorilla gorilla	7	0	0	4	2	8	1	1	0	23	38
Gorilla gorilla diehli	1	0	1	0	0	0	0	0	0	2	3
Gorilla beringei beringei	0	5	12	1	1	8	0	1	2	30	49
Gorilla beringei graueri	2	0	0	0	0	0	0	0	4	6	10

APPENDIX C. Quantitative data

Category	Species	Measurement	Variable	Stimuli	Study Site	Source
Soil Scratching	*G. gorilla gorilla*	465	Soil-scratching traces	Insectivory: [assumed] earthworms and other insects	Nouabalé-Ndoki National Park, ROC	Nishihara and Kuroda 1991
		0.84	Average frequency of traces / km	Insectivory	Nouabalé-Ndoki National Park, ROC	Nishihara and Kuroda 1991
		≤3 cm (width) x 5 cm (length)	Size of excavated particles from soil surface	Undetermined: Particles resembled small roots or tubers	Dzanga-Ndoki National Park, CAR	Cipolletta et al. 2007
Soil Scraping	*G.beringei beringei*	5 meter (length) x 2 meters (width)	Bare soil patch	Geophagy	Volcanoes National Park - Mt. Mikeno, DRC	Schaller 1963
Excavated Chambers and Depressions	*G.beringei beringei*	13 cm - 30 cm (depth) x 13 cm - 25 cm (width)	Excavated holes	Sub-surface foraging for *Cynoglossum amplifolium* roots	Virunga National Park - Kisoro region, DRC	Schaller 1963
		15 cm (length)	Excavated hole	Sub-surface foraging for *Cynoglossum* roots	Virunga National Park - Kisoro region, DRC	Schaller 1963
		8 cm (length)	Diameter of uprooted shrub at stem base	N/A	Volcanoes National Park - Kabara region, DRC	Schaller 1963
	G. beringei graueri	19 cm (depth)	Excavated hole	Insectivory: Ants	Kahuzi - Biega National Park - Itebero region, DRC	Yamagiwa et al. 1991
Excavated Insect Mounds	*G. gorilla gorilla*	54	*Cubitermes sp.* mounds excavated	Insectivory	Lope Reserve, Gabon	Tutin and Fernandez 1983
	G. gorilla gorilla	50 - 200	Small soil fragments from dismantled mounds	Insectivory	Dzanga-Ndoki National Park, CAR	Tutin and Fernandez 1983

APPENDIX C. Continued

Category	Species	Measurement	Variable	Stimuli	Study Site	Source
Excavated Insect Mounds	*G. gorilla gorilla*	1 -4 cm (width)	Size of small soil fragments from dismantled mound	Insectivory	Dzanga-Ndoki National Park, CAR	Tutin and Fernandez 1983
		1 - 3	Large soil fragments from dismantled mounds	Insectivory	Dzanga-Ndoki National Park, CAR	Tutin and Fernandez 1983
		20 - 50 cm (width)	Size of large soil fragments from dismantled mound	Insectivory	Dzanga-Ndoki National Park, CAR	Tutin and Fernandez 1983
		96	*Cubitermes sp.* Mounds broken	Insectivory	Dzanga-Sangha Dense Forest Reserve, CAR	Carroll 1986
	G.beringei beringei	5	*Dorylus sp.* Mounds excavated	Insectivory	Volcanoes National Park - Virunga Volcanoes in Rwanda	Watts 1989
Foot and Knuckle prints	*G.beringei beringei*	14.5 - 16.4 cm (width)	Silverback males knuckle print	Ranging	Volcanoes National Park - Kabara region, DRC	Schaller 1963
		13.5 cm (width)	Blackback male knuckle print	Ranging	Volcanoes National Park - Kabara region, DRC	
		12 - 14 cm (width)	Two females knuckle print	Ranging	Volcanoes National Park - Kabara region, DRC	
		9.5 cm	Juvenile knuckle print	Ranging	Volcanoes National Park - Kabara region, DRC	
		24 - 26.5 cm (length - toes curled under sole	Foot of three silverbacked males	Ranging	Volcanoes National Park - Kabara region, DRC	
		29 cm (length - toes extended)	Foot of three silverbacked males	Ranging	Volcanoes National Park - Kabara region, DRC	

APPENDIX C. Continued

Category	Species	Measurement	Variable	Stimuli	Study Site	Source
Bare/Semi-bare soil bottom terrestrial nest site	*G.beringei beringei*	236	Individual soil nest sites	N/A	Volcanoes National Park - Kabara region, DRC	Schaller 1963
		38 cm (depth)	Soil nest cup	Sleeping	Volcanoes National Park - Kabara region, DRC	Schaller 1963
		13	Soil nests	Sleeping	Kahuzi-Biéga National Park, Mt. Kahuzi region, DRC	Schaller 1963
	G. gorilla gorilla	24	Group nest sites	Night nest	Dzanga-Sangha Reserve, CAR	Remis 1993
		74	Group nest sites	Night nest	Dzanga-Sangha Reserve, CAR	Remis 1993
		578	Individual nest sites	Night nest	Dzanga-Sangha Reserve, CAR	Remis 1993
		105	Group nest sites	Night nest	Dzanga-Sangha Reserve, CAR	Remis 1993
		57	Group nest sites	Night nest	Dzanga-Sangha Reserve, CAR	Remis 1993
		119	Bare soil gorilla group nest sites	Sleeping	Lope Reserve, Gabon	Tutin and Parnell 1995
		121	Individual bare soil gorilla nests	Sleeping	Lope Reserve, Gabon	Tutin and Parnell 1995
		7	Bare soil individual nest site	Sleeping	Dzanga-Ndoki National Park, CAR	Blom et al. 2001
		5	Semi-bare soil individual nest sites	Sleeping	Dzanga-Ndoki National Park, CAR	Blom et al. 2001
		4.3	Average days: Nest life span for a bare soil nest site	Sleeping	Dzanga-Ndoki National Park, CAR	Blom et al. 2001
		19.1	Average days: Nest life span for a semi-bare soil bottom nest site	Sleeping	Dzanga-Ndoki National Park, CAR	Blom et al. 2001

APPENDIX C. Continued

Category	Species	Measurement	Variable	Stimuli	Study Site	Source
Bare/Semi-bare soil bottom terrestrial nest site	*G. gorilla gorilla*	1739	Individual bare soil night nest sites	Sleeping	Dzanga-Ndoki National Park, Mondika Research Center, CAR and ROC	Mehlman and Doran 2002
		95	Bare soil individual night nest sites	Sleeping	Nouabalé-Ndoki National Park, ROC	Sanz et al. 2007
		6	Individual bare soil night nest sites	Sleeping	Moukalaba-Doudou National Park, Gabon	Iwata and Ando 2007
		51	Individual night nest sites	Sleeping	Dja Biosphere Reserve, Cameroon	Willie et al. 2014
Trampling	*G. beringei graueri*	101	Average meters traveled distance - Ant-feeding site to ant-feeding site	Insectivory	Volcanoes National Park - Itebero Region, DRC	Yamagiwa et al. 1991
		136	Average meters traveled distance: Ant - feeding site to ant-feeding site	Insectivory	Volcanoes National Park - Itebero Region, DRC	Yamagiwa et al. 1991
		236	Average meters traveled distance: Ant-feeding site to "other" site	Insectivory	Volcanoes National Park - Itebero Region, DRC	Yamagiwa et al. 1991
		222	Average meters traveled distance: Ant-feeding site to "other" site	Insectivory	Volcanoes National Park - Itebero Region, DRC	Yamagiwa et al. 1991
	G.beringei beringei	10	Square meter trampled area	Ranging	Volcanoes National Park, DRC	Plumptre 1993
		5	Square meter trampled area	Ranging	Volcanoes National Park, DRC	Plumptre 1993

APPENDIX D. Qualitative data

Category	Species	Measurement	Variable	Stimulus	Region	Source
Soil Scratching	*G. gorilla gorilla*	13	Observations of soil scratching behavior	Insectivory: termites	Dzanga-Sangha Dense Forest Reserve, CAR	Carroll 1986
		1	Observation of soil scratching behavior	Insectivory: [assumed] earthworms and other insects	Nouabalé-Ndoki National Park, ROC	Nishihara and Kuroda 1991
		1	Observation of gorilla scratching soil	Insectivory	Nouabalé-Ndoki National Park, ROC	Nishihara and Kuroda 1991
		2	Photographs of soil scratching traces	Insectivory	Nouabalé-Ndoki National Park, ROC	Nishihara and Kuroda 1991
		37	Observed soil scratching bout	Undetermined	Dzanga-Ndoki National Park, CAR	Cipolletta et al. 2007
		13	Observed soil scratching bout	Undetermined: attempts to identify food ingested failed	Dzanga-Ndoki National Park, CAR	
		3-150	Minutes of soil scratching bout	Undetermined: attempts to identify food ingested failed	Dzanga-Ndoki National Park, CAR	
	G. gorilla beringei	30	Minute soil eating bout	Geophagy	Volcanoes National Park - Virunga Volcanoes in Rwanda	Mahaney, Watts, and Hancock 1990
	G. beringei graueri	3	Gorilla group trails with evidence of soil scratching (ant-feeding sites)	Insectivory	Kahuzi-Biega National Park, DRC-Itebero region	Yamagiwa et al. 1991
		6	Individual gorilla trails with evidence of soil scratching (ant-feeding sites)	Insectivory	Kahuzi-Biega National Park, DRC-Itebero region	Yamagiwa et al. 1991

APPENDIX D. Continued

Category	Species	Measurement	Variable	Stimulus	Region	Source
Soil Scraping	*G. beringei beringei*	1	Soil eating site	Geophagy	Volcanoes National Park - Mt. Mikeno, DRC	Schaller 1963
		1	Soil eating site	Geophagy	Volcanoes National Park - Mt. Mikeno, DRC	
		1	Indirect evidence of geophagical behavior	Geophagy	Volcanoes National Park - Mt. Mikeno, DRC	
		1	Soil eating site	Geophagy	Volcanoes National Park - Utu Region	
		1	Observation of geophagical behavior	Geophagy	Volcanoes National Park - Karisoke Research Center, Rwanda	Mahaney, Watts, and Hancock 1990
Excavated Chambers and Depressions	*G. beringei beringei*	1	Observation soil digging	Sub-surface foraging for *Arundinaria alpina* shoots	Volcanoes National Park - Mt. Tshiaberimu	Schaller 1963
		1	Observation soil digging	Sub-surface foraging for root of *Dryopteris*	Volcanoes National Park - Utu Region	
		1	Observation soil digging	Sub-surface foraging for root of *Cynoglossum amplifolium*	Volcanoes National Park - Kabara region, DRC	
		1	Indirect evidence of sub-surface foraging	Sub-surface foraging for root of *Cynoglossum amplifolium*	Volcanoes National Park - Kabara region, DRC	

APPENDIX D. Continued

Category	Species	Measurement	Variable	Stimulus	Region	Source
Excavated Chambers and Depressions	*G. beringei beringei*	1	Observation soil digging	Sub-surface foraging for tuber of *Manihot*	Volcanoes National Park - Utu Region	Schaller 1963
		1	Observation of soil displacment	Display behavior	Volcanoes National Park - Kabara region, DRC	
			Photograph of excavatd hole	Sub-surface foraging	Virunga National Park - Kisoro region, DRC	
		1	Geophagy mining site	Geophagy	Volcanoes National Park - Mt. Visoke, Rwanda	Fossey 1983
		1	Observation of soil digging	Geophagy	Volcanoes National Park - Mt. Visoke, Rwanda	Fossey 1983
		1	Observation of soil digging	Sub-surface foraging for ants	Volcanoes National Park - Karisoke Research Center, Rwanda	Watts 1989
		1	Geophagy mining site	Geophagy	Lopé Reserve, Gabon	Williamson et al. 1990
		1	Geophagy mining site	Geophagy	Volcanoes National Park - Karisoke Research Center, Rwanda	Mahaney, Aufreiter, and Hancock 1995
	G. gorilla diehli	1	Observation of soil display	Display behavior	Kagwene Gorilla Sanctuary, Cameroon	Wittiger and Sunderland-Groves 2007
Bare / Semi - Bare Soil Bottom Terrestrial Nest	*G. beringei beringei*	1	Observation of soil nest construction	Resting	Volcanoes National Park - Kabara region, DRC	Schaller 1963
		1	Indirect evidence of gorilla group nest site on turf and soil on an "open slope for two consecutive nights" (174)	Sleeping	Volcanoes National Park - Kabara region, DRC	

APPENDIX D. Continued

Category	Species	Measurement	Variable	Stimulus	Region	Source
Bare / Semi - Bare Soil Bottom Terrestrial Nest	*G. beringei beringei*	1	Indirect evidence of individual soil nest sites	Resting	Volcanoes National Park - Kabara region, DRC	Schaller 1963
		1	Photographed soil bottom nest site	Resting / Sleeping	Volcanoes National Park - Kabara region, DRC	
	G. gorilla gorilla	2	Observed evidence of bare soil nest sites	Protection from thunderstorm	Lopé Reserve, Gabon	Tutin and Parnell 1995
Hand/Knuckle and Foot Prints	*G. gorilla gorilla*	54	Observed gorilla trails with clear foot or knuckle prints	Ranging	Lope Reserve, Gabon	Tutin and Fernandez 1983
		13	Days documented knuckle prints	Soil scratching	Dzanga-Ndoki National Park, CAR	Cipolletta et al. 2007
	G. beringei beringei	465	Observations of hand or footprints	Insectivory	Nouabalé-Ndoki National Park, ROC	Nishihara and Kuroda 1991
Excavated Insect Mound	*G. beringei beringei*	5	Observed driver ant mound excavation and feeding bouts	Insectivory	Volcanoes National Park - Karisoke Research Center, Rwanda	Watts 1989
		3	Partially observed mound excavation and feeding bout	Insectivory	Volcanoes National Park - Karisoke Research Center, Rwanda	
		8	Minute driver ant mound excavating bout	Insectivory	Volcanoes National Park - Virunga Volcanoes in Rwanda	
		10	Minute driver ant mound excavating bout	Insectivory	Volcanoes National Park - Virunga Volcanoes in Rwanda	

APPENDIX D. Continued

Category	Species	Measurement	Variable	Stimulus	Region	Source
Excavated Insect Mound	*G. beringei beringei*	22	Minute driver ant mound excavating bout	Insectivory	Volcanoes National Park - Virunga Volcanoes in Rwanda	Watts 1989
		30	Minute driver ant mound excavating bout	Insectivory	Volcanoes National Park - Virunga Volcanoes in Rwanda	
		35	Minute driver ant mound excavating bout	Insectivory	Volcanoes National Park - Virunga Volcanoes in Rwanda	
		12.8	Visits (total average visits) to driver ant mound	Insectivory	Volcanoes National Park - Virunga Volcanoes in Rwanda	
	G. gorilla gorilla	294	Observations of termite mound excavations	Insectivory	Dzanga-Ndoki National Park, CAR	Cipolletta et al. 2007
		214	Days of observed gorilla group at mound feeding on termites	Insectivory	Dzanga-Ndoki National Park, CAR	
		1	Observed termite mound excavation technique	Insectivory	Dzanga-Ndoki National Park, CAR	
		23	Observed feeding bouts	Insectivory	Dzanga-Ndoki National Park, CAR	
		47	Minutes (median value) termite feeding bout	Insectivory	Dzanga-Ndoki National Park, CAR	
		419	*Cubitermes* mound built against tree visits	Insectivory	Dzanga-Ndoki National Park, CAR	
		0.18	*Cubitermes* mound visits dug out of the ground	Insectivory	Dzanga-Ndoki National Park, CAR	

APPENDIX D. Continued

Category	Species	Measurement	Variable	Stimulus	Region	Source
Excavated Insect Mound	*G. gorilla gorilla*	14	*Cubitermes* free-standing mound vists	Insectivory	Dzanga-Ndoki National Park, CAR	Cipolletta et al. 2007
Tool Use	*G. gorilla gorilla*	1	Observation of female gorilla using detached branch as walking stick	Postural support	Nouabalé-Ndoki National Park, ROC	Breuer, Ndoundou-Hockemba, and Fishlock 2005
Trunk Uprooting	*G. beringei beringei*	1	Observed silverback uprooting dead *Vernonia adolfi-fredericii* trunk	Insectivory	Volcanoes National Park - Karisoke Research Center, Rwanda	Watts 1989
	G. gorilla gorilla	1	Observation of female detaching a leafless trunk of dead shrub	Support while dredging for aquatic herbs	Nouabalé-Ndoki National Park, ROC	Breuer, Ndoundou-Hockemba, and Fishlock 2005
Trampling	*G. beringei beringei*	1.5	Days gorillas spent in bamboo or woodland habitat.	Foraging and ranging	Volcanoes National Park, Rwanda	Watts 1989
		13	Individuals in one gorilla group caused 15 square meter area of trampling	Ranging	Volcanoes National Park, Rwanda	Plumptre 1993
	G. beringei graueri	1	Gorilla group trail between ant-feeding sites	Insectivory	Volcanoes National Park - Itebero Region, DRC	Yamagiwa et al. 1991
		5	Solitary gorilla trails between 2 seperate ant-feeding sites	Insectivory	Volcanoes National Park - Itebero Region, DRC	
		10	Gorilla group trails between ant-feeding site and "other" site	Insectivory	Volcanoes National Park - Itebero Region, DRC	
		13	Solitary gorilla trails between ant-feeding site and "other" site	Insectivory	Volcanoes National Park - Itebero Region, DRC	

APPENDIX E. Vegetation associated with zoogeomorphic activity

Zoogeomorphic Relevance	Vegetation/Habitat	Notes	Source
Terrestrial nest site	*Aframomum sulcatum*	High nest densities and largest group sizes in this habitat, pith of this species is preferred, primary food out of 33 species of gorilla plant food items collected by author, comprised 29% of all gorilla food observations.	Carroll 1986
Soil-scratching	*Gilbertiodendron dewevrei*	Sub-surface foraging for insectivory.	
Termite mound excavation	Savannah habitat	Insectivory-96 termite mounds observed broken by gorillas, savannah termites account for 17% of total gorilla food items observed.	
Soil-scratching	*Gilbertiodendron dewevrei*	Riverine area (especially the swamp) of this habitat type, sub-surface insectivory for [found after imitating gorilla scratching behavior] insects, termites, ants, grubs, earthworms, soil-scratching trace photographed near root of *G. dewevrei*	Nishihara and Kuroda 1991
Bare soil nest site	Marantaceae	Bare soil nests most frequently built in this habitat during dry seasons.	Mehlman and Doran 2002
Soil-scratching	*Gilbertiodendron* forest	Soil scratching traces found with cleared leaf litter and accompanied with "numerous" (466) knuckle prints.	Cipolletta et al. 2007
Sub-surface foraging	*Arundinaria alpina* (bamboo)	Young shoots dug up were approximately ≤ 13 cm. 'moderately' consumed.	Schaller 1963

APPENDIX E. Continued

Zoogeomorphic Relevance	Vegetation/Habitat	Notes	Source
Sub-surface foraging	*Dryopteris*	Root and base of stem eaten. Infrequently consumed.	Schaller 1963
Group night nest site	*Hagenia*	4 individual night nests constructed against trees.	Schaller 1963
Nest construction	*Vernonia*	Shrub uprooted at base and used for nest site construction material.	Schaller 1963
Sub-surface foraging	*Cynoglossum geometricum* (herb)	Root and lower part of stem eaten. Moderately consumed.	Schaller 1963
Sub-surface foraging	*Lobelia wollastonii* (herb)	Root and base of leaf cluster eaten. Moderately consumed	Schaller 1963
Sub-surface foraging	*Lobelia giberroa* (herb)	Stem consumed. Infrequently used.	Schaller 1963
Sub-surface foraging	*Chaerefolium silvestre* (herb)	Root and lower part of stem eaten. Moderately consumed.	Schaller 1963
Sub-surface foraging	*Cynoglossum amplifolium* (herb)	Root eaten. Moderately consumed.	Schaller 1963
Sub-surface foraging	*Rumex ruwenzoriensis* (herb)	Root and lower part of stem eaten. Moderately consumed.	Schaller 1963
Sub-surface foraging	*Arundinaria alpina (bamboo)*	Young stem and shoot eaten. Heavily consumed.	Schaller 1963
Sub-surface foraging	*Lobelia wollastonii (herb)*	Root and base of leaves consumed. Moderately consumed.	Schaller 1963
Sub-surface foraging	*Cynoglossum geometricum* (herb)	Root eaten. Heavily consumed.	Schaller 1963

APPENDIX E. Continued

Zoogeomorphic Relevance	Vegetation/Habitat	Notes	Source
Sub-surface foraging	*Cynoglossum amplifolium* (herb)	Root eaten. Heavily consumed.	Schaller 1963
Foraging	*Rumex nepalensis* (herb)	Stem and leaf eaten.	Schaller 1963
Foraging	*Rumex usambarensis* (herb)	Stem eaten.	Schaller 1963
Foraging	*Carduus afromontanus* (herb)	Stem and leaf eaten. Moderately consumed.	Schaller 1963
Foraging	*Laportea alatipes* (herb)	Stem eaten. Moderately consumed.	Schaller 1963
Foraging	*Kniphofia grantii* (herb)	Stem eaten. Infrequently used.	Schaller 1963
Foraging	*Droquetia iners* (vine)	Stem and leaves consumed.	Schaller 1963
Foraging	*Piper capense* (vine)	Stem and bark eaten.	Schaller 1963
Sub-surface foraging	*Cyathea deckenii* (fern)	Shoot and pith of frond eaten. Heavily consumed.	Schaller 1963
Foraging	*Rumex usambarense* (herb)	Stem eaten. Moderately consumed.	Schaller 1963
Foraging	*Fleurya ovalifolia* (vine)	Stem eaten. Moderately consumed.	Schaller 1963
Foraging	*Pennisetum purpureum* (grass)	Shoots and young stem eaten. Heavily consumed.	Schaller 1963
Foraging	*Rumex bequarertii* (herb)	Stem eaten. Moderately consumed.	Schaller 1963

APPENDIX E. Continued

Zoogeomorphic Relevance	Vegetation/Habitat	Notes	Source
Foraging	*Rumex bequarertii* (herb)	Stem eaten. Moderately consumed.	Schaller 1963
Foraging	*Rumex ruwenzoriensis* (herb)	Stem consumed. Infrequently used.	Schaller 1963
Foraging	*Peucedanum linderi* (herb)	Stem consumed.	Schaller 1963
Foraging	*Pennisetum purpureum (grass)*	Stem consumed.	Schaller 1963
Sub-surface foraging	*Arundinaria alpina (bamboo)*	Young stem and shoot eaten. Heavily consumed.	Schaller 1963
Foraging	*Arundinaria alpina (bamboo)*	Stem and shoot eaten.	Schaller 1963
Foraging	*Pennisetum purpureum (grass)*	Stem eaten.	Schaller 1963
Foraging	*Dryopteris spp.* (fern)	Stem eaten.	Schaller 1963
Foraging	*Marattia fraxinea* (fern)	Inside of stem eaten.	Schaller 1963
Foraging	*Marantochloa leucantha* (herb)	Young shoot eaten. Moderately consumed.	Schaller 1963
Foraging	*Palisota sp.* (herb)	Base of main stem eaten. Moderately consumed.	Schaller 1963
Sub-surface foraging	*Arundinaria alpina* (bamboo)	Feed on bamboo shoots upon shooting season.	Fossey 1983
Geophagy sites	*Hagenia-Hypericum woodland zone*	"Several" soil eating sites known to be visited frequently by gorillas.	Mahaney, Watts, and Hancock 1990

APPENDIX E. Continued

Zoogeomorphic Relevance	Vegetation/Habitat	Notes	Source
Trampling	*Senecio mariettae*	Gorilla trampling mainly caused damage to this habitat. Author noted this species is not a food item. Trampling found in saddle between Mt. Visoke and Mt. Karisimbi	Plumptre 1993
Trampling	*Hagenia-Hypericum* woodland	Evidence of trampling found in saddle between Mt. Visoke and Mt. Karisimbi.	Plumptre 1993
Trampling	*Arundinaria alpina* (bamboo)	10 square meter area showed evidence of trampling by gorillas.	Plumptre 1993
Geophagy site	*Hagenia-Hypericum*	Site located at 300m a.s.l., bamboo shoots may form >90% of mountain gorilla diet.	Mahaney, Aufreiter, and Hancock 1995
Sub-surface foraging	*Lobelia sp.*	Pith and root of *Lobelia*, contains alkaloids.	
Sub-surface foraging	*Senecio sp.*	Pith and root of *Senecio,* contains alkaloids.	
Trampling	*Lobelia*	This habitat occurs at higher altitudes where vegetation grows slower. Author noted gorillas visited these areas less than 5 months. Gorillas spent a minimum of 1.5 days in this habitat.	Watts 1998
Trampling	*Senecio*	Gorilla main food sources located in this habitat. Author noted that frequent visits by gorillas for greater than 5 months results in slower regeneration rate. Gorillas spent a minimum of 1.5 days in this habitat.	Watts 1998
Sub-surface foraging	*Urtica massaica*	Root consumed	McNeilage 2001

APPENDIX E. Continued

Zoogeomorphic Relevance	Vegetation/Habitat	Notes	Source
Sub-surface foraging	*Carduus leptocanthus*	Root consumed.	McNeilage 2001
Sub-surface foraging	*Carduus kikuyorum*	Root consumed.	McNeilage 2001
Sub-surface foraging	*Vernonia adolfi-fredricii*	Root consumed.	McNeilage 2001
Sub-surface foraging	*Laportea alatipes (herb)*	Root consumed.	McNeilage 2001
Sub-surface foraging	*Crassocephalum ducis-aprutii*	Root consumed.	McNeilage 2001
Sub-surface foraging	*Peucedanum linderi (herb)*	Root consumed.	McNeilage 2001
Sub-surface foraging	*Arundinaria alpina (bamboo)*	Shoot consumed.	McNeilage 2001
Sub-surface foraging	*Lobelia giberroa (herb)*	Root consumed.	McNeilage 2001
Sub-surface foraging	*Senecio johnstonii*	Root consumed.	McNeilage 2001
Sub-surface foraging	*Carduus nyassanus*	Root consumed.	McNeilage 2001
ant mound excavation/sub-surface foraging	*Aframomum latifoliam*	Gorillas unlikely to feed on plant food items within ant-feeding sites; per author, only once was gorilla seen eating on pith and fruit of this species.	Yamagiwa et al. 1991
Ant mound excavation	Neoboutonia Forest and *Arundinaria alpina (bamboo)*	Adult male gorilla observed using his left hand to collect driver ants (*Dorylus* sp.) from hole in the ground, female gorilla (within ~6m away) inserted her hand into the same hole after male gorilla ran away.	Kinani and Zimmerman, 2015

APPENDIX F. Insects associated with zoogeomorphic activity

Species	Insect Species	Study Area	Notes	Source
Gorilla gorilla gorilla	*Cubitermes sp.*	Gabon	Small termite (5 to 10 mm long) which builds grey terrestrial mounds (50 to 100 cm high) against living tree trunks. Tiered layers make up the uppermost part of the mound and is relatively soft making it easy to break apart.	Tutin and Fernandez 1983
Gorilla gorilla gorilla	*Cubitermes sp.*	Dzanga-Sangha Dense Forest Reserve, CAR		Carroll 1986
Gorilla beringei graueri	*Ponerinae Family* *1. Euponena (Mesopanera) subiridescens* *2. Odontomachus troglodytes* *3. Odontomachus Assiensis* *4. Pachycondyla (Bothroponera) talpa (Andre)* *5. Pachycondyla (Bothroponera) sp.* *6. Palotothyreus tarsalus (Fabricius)*	Itebero region, DRC; between Luka and Utu Rivers	Ants collected at feeding sites of gorillas. Sites found on a total of 9 gorilla trails (3 group trails and 6 individual solitary male trails). Sites indicated by soil scratching traces.	Yamagiwa et al. 1991
Gorilla gorilla gorilla	*Oecophilla longinoda* (weaver ant)	Lope Reserve, Gabon	Mounds constructed in trees and made from leaves. Gorillas generally have to climb trees to access ants.	Tutin and Fernandez 1992
Gorilla gorilla gorilla	*Toracotermes*	Dzanga-Ndoki National Park	15 percent of free-standing mounds visited and dismantled by gorillas.	Cipolletta et al. 2007
Gorilla beringei beringei	*Dorylus sp.* (driver ant)	Volcanoes National Park, Rwanda		Kinani and Zimmerman, 2015

APPENDIX G. Geology and minerals associated with zoogeomorphic activity

Species	Study Site	Physio - Chemical Properties	Zoogeomorphic Relevance	Notes	Source
G. gorilla beringei	Volcanoes National Park - Karisoke Research Center, Rwanda	Calcium, potassium rich soil	geophagy sites	Direct observation occurred during the dry months. Group 4 obtained loose dirt mainly from sandy slides where swallows bathe and nest (during the dry seasons)	Fossey 1983
G. gorilla beringei	Volcanoes National Park - Karisoke Research Center, Rwanda	Fe, Na, and Br content, high clay content in soil	geophagy sites	Visits last up to 30 minutes, all group members excluding infants excavate and eat soil, Br-twice as abundant in sampled soil ingested by gorillas potentially making it a significant factor in geophagia, Na-low Na content in regional vegetation so Na rich soil used as a mineral supplement food, Fe-potentially used in erythrocyte production especially in high elevation species, clay rich regolith potentially functions as a kaopectate aiding in the digestion of tannin rich flora	Mahaney, Watts, and Hancock 1990
G. gorilla beringei	Volcanoes National Park - Mt. Visoke, Rwanda	halloysite clay minerals, kivites and leucites	geophagy sites	Study region composed mostly of kivite (dark colored and olivine) rich leucite (subsoil C horizons), these outcrops found mostly within the saddle areas and along slopes of the major volcanoes, ingested mostly in the dry season.	Mahaney 1993

APPENDIX G. Continued

Species	Study Site	Physio - Chemical Properties	Zoogeomorphic Relevance	Notes	Source
G. gorilla beringei	Volcanoes National Park - Karisoke Research Center, Rwanda	Halloysite-found in subsoil clay eaten by gorillas, sandy to silty loam texture soil,	geophagy [cavern] sites	Material mined by gorillas is transported volcanic rock mainly leucite or K-rich weathered sediments on the flanks of Visoke Volcano at 3000 m a.s.l.	Mahaney, Aufreiter, and Hancock 1995
G. gorilla beringei	Volcanoes National Park - Utu Region	Quartz (small rocks) with exposed layer of white and crumbly soil	geophagy	Located along trail passing through shallow ravine with one side of partially bare and exposed soil layer.	Schaller 1963
G. gorilla beringei	Volcanoes National Park - Mt. Mikeno, DRC	P, S, N, Ca, Mg, K, Mn, Na	geophagy	Observed consumed by two gorilla groups with a total of 45 individuals.	Schaller 1963
G. gorilla beringei	Bwindi Impenetrable National Park, Uganda	Ca, P, Mg, K, Na, Fe, Zn, Cu, Mn	Sub-surface forage - root	Analysis revealed high concentrations of Na content in roots. Authors noted sample of 103 plants but did not explicitly name the plant root came from.	Cancelliere et al. 2014
G. gorilla beringei	Bwindi Impenetrable National Park, Uganda	K	Forage - stem	Analysis revealed high concentrations of K content in roots. Authors noted sample of 103 plants but did not explicitly name the plant stem came from.	Cancelliere et al. 2014

APPENDIX H. Topography associated with zoogeomorphic activity

Location	Measured	Signature	Species	Region	Source
Slope (degrees)	30	36 individual night ground nest (1 group nest)	*Gorilla beringei beringei*		Schaller 1963
	10	10 individual night ground nest (1 grp. nest site)	*Gorilla beringei beringei*	Utu region between Utu and Niabembe	Schaller 1963
	40	8 individual night ground nest (1 grp. nest site)	*Gorilla beringei beringei*	Kisoro Virunga Volcanoes	Schaller 1963
	15	7 individual night ground nest (grp. nest site)	*Gorilla beringei beringei*	Kisoro Virunga Volcanoes	Schaller 1963
	30	18 individual night nest sites	*Gorilla beringei beringei*	Kabara Region	Schaller 1963
	flat	14 individual night nest site	*Gorilla beringei beringei*	Kabara Region	Schaller 1963
	flat	12 individual night nest sites	*Gorilla beringei beringei*	Kabara Region	Schaller 1963
	flat - 10	11 individual night nest sites	*Gorilla beringei beringei*	Kabara Region	Schaller 1963
	20	14 individual night nest site	*Gorilla beringei beringei*	Kabara Region	Schaller 1963
	flat - 10	15 individual night nest sites	*Gorilla beringei beringei*	Kabara Region	Schaller 1963
	25	13 individual night nest	*Gorilla beringei beringei*	Kabara Region	Schaller 1963
	flat - 25	14 individual night nest site	*Gorilla beringei beringei*	Kabara Region	Schaller 1963
	15	3 individual night nest sites	*Gorilla beringei beringei*	Kayonza Forest	Schaller 1963
	10	12 individual night nest sites	*Gorilla beringei beringei*	Kayonza Forest	Schaller 1963
	flat	1 individual night nest site	*Gorilla beringei beringei*	Utu region near Kasese	Schaller 1963
	15	3 individual night nest sites	*Gorilla beringei beringei*	Mt. Tshiaberimu	Schaller 1963
	30	9 individual night nest sites	*Gorilla beringei beringei*	Mwenga - Fizi region near Mulenge	Schaller 1963
	30	24 individual night nest sites	Gorilla beringei beringei	Kabara Region	Schaller 1963
	15 - 20	14 individual night nest site	*Gorilla beringei beringei*	Kabara Region	Schaller 1963

APPENDIX H. Continued

Location	Measured	Signature	Species	Region	Source
Slope (degrees)	25 - 50	Number of nest sites not indicated	*Gorilla beringei beringei*	Kabara Region	Schaller 1963
Slope (location)	3	Group nest sites	*Gorilla beringei beringei*	Kayonza Forest	Schaller 1963
	1	Individual night nest site	*Gorilla beringei beringei*	Kabara Region	Schaller 1963
	4	Gorilla group feeding trails between 2 separate ant-feeding sites	*Gorilla beringei graueri*	Itebero Region, DRC	Yamagiwa et al. 1991
	6	Individual solitary male feeding trails between ant-feeding sites and "other" (250) sites	*Gorilla beringei graueri*	Itebero Region, DRC	Yamagiwa et al. 1991
	23	Group ground nest sites	*Gorilla beringei graueri*	Mt. Kahuzi region, DRC	Casimir 1979
	157	Individual ground nests	*Gorilla beringei graueri*	Mt. Kahuzi region, DRC	Casimir 1979
	1	Geophagy site	*Gorilla beringei beringei*	Parc National des Volcans, Rwanda - Karisoke Research Centre	Mahaney, Watts, and Hancock 1990
Tree (adjacent to)	5	2 individual Silverback nest sites, 3 blackback or female or juvenile nest sites	*Gorilla beringei beringei*	Kabara Region	Schaller 1963
	17	Silverback night nest	*Gorilla beringei graueri*	Mt. Kahuzi region, DRC	Casimir 1979
	23	Mother and infant night nest	*Gorilla beringei graueri*	Mt. Kahuzi region, DRC	Casimir 1979

APPENDIX H. Continued

Location	Measured	Signature	Species	Region	Source
Ravine	1	Geophagy site	*Gorilla beringei beringei*	Utu Region	Schaller 1963
Ridge	1	Geophagy mining site	*Gorilla beringei beringei*	Mt. Visoke, Rwanda	Fossey 1983
	2	Gorilla group feeding trails between 2 separate ant-feeding sites	*Gorilla beringei graueri*	Itebero Region, DRC	Yamagiwa et al. 1991
	6	Individual solitary male feeding trails between ant-feeding sites and "other" (250) sites	*Gorilla beringei graueri*	Itebero Region, DRC	Yamagiwa et al. 1991
Saddle	5	Square meter trampled area	*Gorilla beringei beringei*	Parc National des Volcans, Rwanda - Saddle between Mt. Visoke and Mt. Karisimbi	Plumptre 1993

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