Ecological Role of Dry-Habitat Chimpanzees (*Pan troglodytes schweinfurthii*) at Issa, Ugalla, Tanzania

by

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ABSTRACT

Identifying the ecological role, or niche, that a species occupies within their larger community elucidates environmental adaptability and evolutionary success. This dissertation investigates the occupied niche of chimpanzees (*Pan troglodytes schweinfurthii*) living in an open, dry savanna-woodland environment by examining patterns of resource use and interspecific interactions. Data were collected October 2010—November 2011 at Issa, in the Ugalla region of western Tanzania, which is one of the driest, most open, and seasonal habitats inhabited by chimpanzees.

Unlike most primatological studies which employ methods that include focal follows, this study focused instead on observing 'resource patches' for chimpanzees. Patch focals allow for the observation of all animals within a study area; capture resources that are not used by the study species; and are particularly well suited for unhabituated communities. In order to better understand relationships between environment and behavior, data collected at Issa are compared with published data from other chimpanzee populations.

Issa chimpanzees were expected to have broader resource use than forest chimpanzees, as well as increased competition with other fauna, due to fewer available resources. However, in contrast to the assumption of food scarcity in dry habitats, dietary resources were available throughout the year. Like other populations, the diet of Issa chimpanzees consisted of mostly fruit, but unlike at other sites, the majority of plants consumed were woodland species. Additionally, although chimpanzees and other fauna shared spatial and dietary resources, there was only nominal overlap. These results point to extremely low levels of indirect competition between chimpanzees and other fauna.

Despite extensive study of forest chimpanzees, little is known about their role within their faunal community in open, dry habitats, nor about how greater seasonality affects resource use. This project addresses both of these important issues and fosters novel approaches in anthropological studies, especially in reference to chimpanzee ecology and evolution. Understanding current chimpanzee behavioral relationships with their environments shapes hypotheses about their pasts, and also informs predictions about behaviors of similar taxa in paleo-environments. Lastly, examining the ecological role of chimpanzees within their larger communities will influence the formation of, as well as evaluate, conservation strategies.

For my mother,
who never stopped encouraging me to ask questions, and who wholeheartedly supports
all of my scientific endeavors, no matter how far from home they may take me

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CHAPTER 1: INTRODUCTION

It is critical to determine the ecological role, or niche, that primate species occupy within their larger communities in order to fully understand how these species are adapted to and manipulate their environment in ways that make them evolutionarily successful (Connell, 1983; Schoener, 1983; Waser, 1987; Tokeshi, 1999). Community ecology studies that explore these ecological roles can determine associations between particular behaviors and certain environments, each of which is composed of both a specific vegetative habitat and a set of sympatric faunal species. These associations, in turn, can be used to predict changes in animal behavior due to either natural or anthropogenic alterations of the environment (Strier, 1997; Cowlishaw and Dunbar, 2000). Additionally, these links between behavior and environment can be used to make inferences about the behaviors of fossil species in paleo-communities that lived in similar environments (Fleagle, 1999; Nunn and van Schaik, 2002; Reed, 2002).

Chimpanzees are ideal study subjects for community ecology research because they use and survive in a wide range of habitats. Across study sites, these provide the necessary variation in both behaviors and environments required to investigate and compare the relationships between these two sets of factors. There is a wealth of information about chimpanzees that live in closed, wet forested sites (e.g., Budongo: Reynolds, 2005; Bwindi: Stanford and Nkurunungi, 2003; Kibale: Ghiglieri, 1984; Lope: Tutin et al., 1997; Tai: Boesch and Boesch-Achermann, 2000) and slightly more open, drier sites (e.g., Gombe: Goodall, 1986; Mahale: Nishida, 1990), but little is known about chimpanzees that live in very dry savanna-woodland habitats (e.g., Assirik: McGrew et al., 1981; Bafing: Duvall, 2000; Fongoli: Pruetz et al., 2002; Semliki: Hunt and McGrew, 2002; Ugalla: Hernandez-Aguilar, 2006).

Characterizing the niche of dry-habitat chimpanzee populations is a necessary step towards a better understanding of overall chimpanzee ecology, which can then be used to provide important insights into hominid (i.e., great ape and human) ecology and evolution. This is especially pertinent to the study of human evolution, as chimpanzees are often used as referential models for early hominins (Kortlandt, 1983; Susman, 1987; Moore, 1992, 1996; Zihlman, 1996), and these "marginal" dry-habitat chimpanzees in particular, are found in habitats that are similar to those in which early hominins (e.g., *Australopithecus, Ardipithecus*) are thought to have evolved (Stanley, 1992; Reed, 1997; Wynn, 2000; Aronson et al., 2008; Le Fur et al., 2009; White et al., 2009). Therefore, links between the environment and behavior of dry-habitat chimpanzees will provide a framework for testing hypotheses regarding the seemingly analogous ecological role of many early hominins.

My dissertation research addresses the ecological role, or niche, occupied by chimpanzees (*Pan troglodytes schweinfurthii*) living in an open, dry habitat in western Tanzania. More specifically, I test hypotheses pertaining to the associations between arid, open environments and the main components of the chimpanzee niche: (1) patterns of resource use (space and food) and (2) interspecific interactions. In order to better elucidate relationships between environment and behavior, data collected at the dry-habitat site of Issa are compared with published data from other chimpanzee populations.

The fundamental niche of chimpanzees includes a wide range of habitat types, sympatric species, social organizations, behavioral interactions, and patterns of resource use. Therefore, it is critical to determine the actual set of conditions, or realized niche, that each chimpanzee population occupies in order to comprehend the adaptability and functioning of these unique dry-habitat chimpanzee populations. This requires research that encompasses both habitat and sympatric fauna, rather than focusing solely on chimpanzees. Non-primate species must also not be ignored, as these species can greatly influence the socio-behavioral ecology of primates by competing for food and space.

Most primatological studies employ methodologies that include actively following the species of interest. However, focal follows are insufficient for community ecology studies since they overlook crucial phenomena occurring when focal species are absent. My dissertation research focuses instead on observing resource patches in chimpanzee habitat. Patch focals allow for the observation of all animals within a study area; elucidate resources that are not used by the study species; and are particularly well suited for unhabituated communities.

This dissertation is organized into nine chapters. Chapter 2 provides important concepts and terminology relevant to community ecology studies, and discusses how these concepts can be applied to chimpanzee populations. Specific hypotheses and predictions for my research are given at the end of the chapter. Chapters 3 and 4 describe the study site and methods used during this study, with a particular emphasis on the utility of patch focals as compared to focal follows of species. The use of particular resources is influenced by their distribution and availability, which is largely determined by climatic factors such as rainfall and temperature. Chapter 5 describes the climate and resource availability at Issa during this study. Use of spatial and dietary resources by Issa chimpanzees is provided in Chapter 6, while resource use by other Issa fauna is given in

Chapter 7. The community ecology of Issa chimpanzees is better contextualized when compared with other chimpanzee communities. Such comparisons are made and summarized in Chapter 8. Finally, overall conclusions and the broader implications of my dissertation research are discussed in Chapter 9.

CHAPTER 2: BACKGROUND

COMMUNITY ECOLOGY

Community ecology is broadly defined as the study of interactions between an assemblage of species populations (i.e., the community) and the surrounding environment. More specifically, this discipline focuses on the distribution, abundance, and behavioral interactions within and between species, and how all of these factors are influenced by the habitat in which these species live. The availability of space and nutrients, and the consistency of this supply, differs both within and between habitats. These environmental constraints influence community assembly by restricting which species become established at the site, and by affecting interactions among existing community members (Danielson, 1991; Belyea and Lancaster, 1999). For example, researchers have found that an increase in neotropical primate richness is strongly correlated with increasing rainfall and forest cover, and latitudes closest to the equator (Peres and Janson, 1999). Additionally, primate community biomass has been shown to vary with habitat type, even when these habitats have similar seasonality and amounts of rainfall. This demonstrates that even small differences in plant species diversity, productivity, and quality can influence community biomass (Gupta and Chivers, 1999). Therefore, in studying the community ecology of any species, the habitat in which the species lives must be adequately examined, often on a very detailed scale.

SOME IMPORTANT ECOLOGICAL FACTORS

HABITATS

There is no single agreed upon definition of a habitat, but perhaps the most basic, and therefore most widely applicable, definition was given by Danielson (1991) who considers a habitat to be a, “combination of biotic and/or abiotic features that provides a useful means of broadly classifying existing conditions into distinct types.” The features that are considered to be “useful” differ from one scientist to the next, but tend to include mean annual rainfall, mean daily temperature, latitude, seasonality, or a combination of these variables (Wolda, 1986). Even more predominant in the scientific literature is the use of the dominant vegetation structure to classify an environment (e.g., forest, grassland, wetland), as plant communities often determine the physical structure of a habitat, and therefore, have a large influence on the distributions and interactions of faunal communities within that habitat (Tews et al., 2004). However, plant communities are affected by abiotic factors (e.g., temperature, precipitation, soil properties), so it is ultimately these variables that classify habitats.

Groupings of natural communities that are broadly similar in vegetation structure are called biomes and can be split into four major structural classes: (1) forest, which contains tall trees with a continuous canopy; (2) woodland grading into shrubland, typified by small, more widely spaced trees and an abundance of undergrowth; (3) savanna, grassland, and savanna-mosaic, which are all dominated by grasses and associated with highly seasonal rainfall; and (4) desert and semidesert scrub with sparse, low growing shrubs and other plants interspersed with large patches of exposed soil (Richard, 1985; Oates, 1987; Sayer, 1992; Fleagle, 1999; Mistry, 2000). These categories can be further broken down based on their phenology, climate, geology, and/or human usage into types such as primary rain forest, secondary rain forest, or gallery forests; the first two classified by plant succession and the latter only occurring around rivers (Ganzhorn, 2003).

These major biomes are not randomly distributed across the globe, but follow general latitudinal and longitudinal patterns (Figure 2-1), such as rainforests being located mostly around the equator. Nonhuman primates are found on five of the seven continents, typically inhabiting (but not limited to) land areas with tropical climates that are located between the Tropics of Cancer and Capricorn (23.5° N and S, respectively). Within the primates, the apes are most closely associated with tropical moist forests and rain forests, but their habitats cover a wide range of environmental variables including altitude, rainfall, vegetative productivity, and seasonality (Caldecott, 2005; Caldecott and Kapos, 2005).

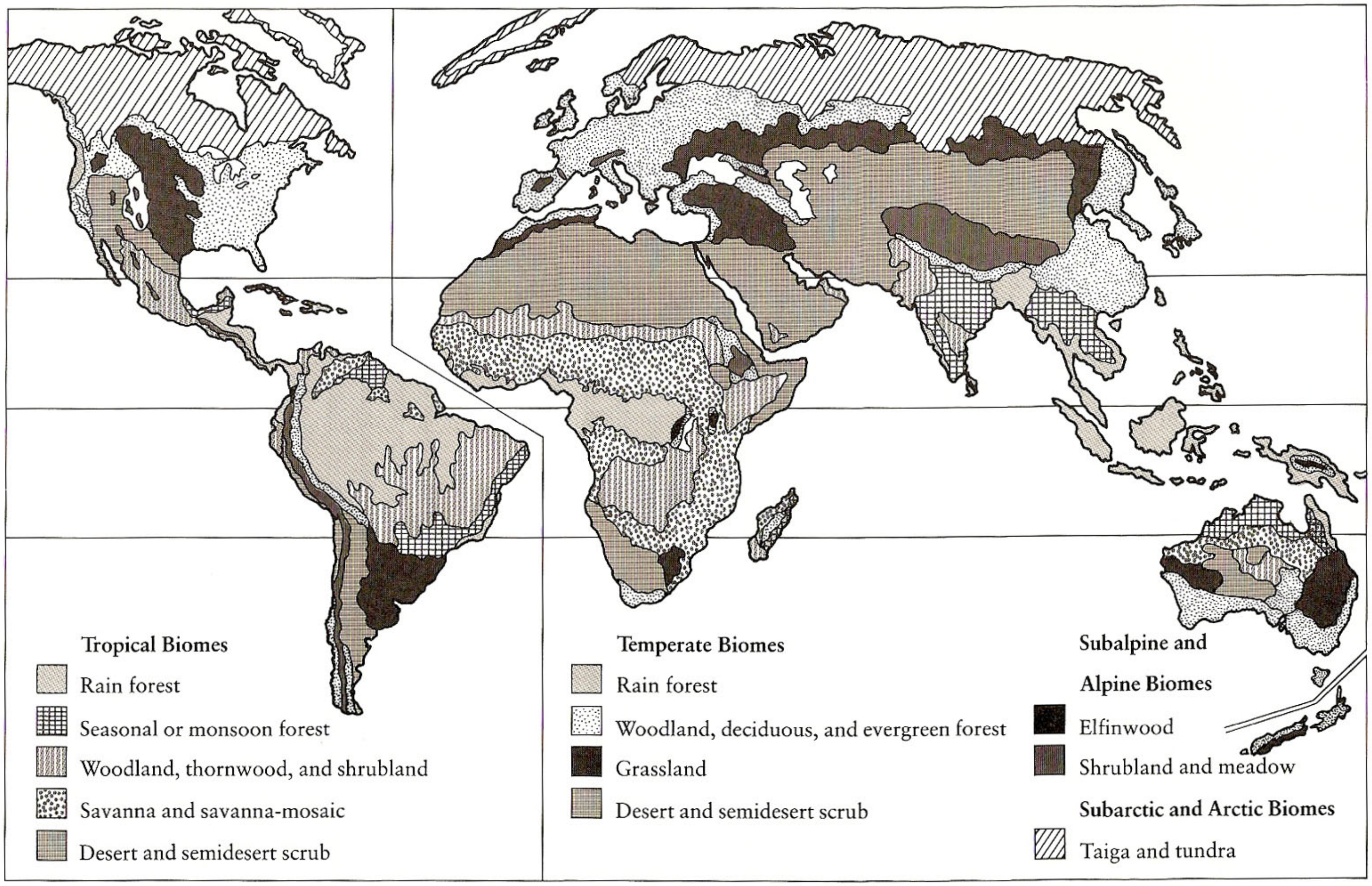


Figure 2-1. Distribution of biomes across the globe (from Richard, 1985).

RESOURCE DISTRIBUTION

As described above, habitats are the result of a combination of biotic and abiotic features. One of the most important characteristics of a habitat is its heterogeneity, or the variability of resources within time and space. A resource can be defined as, "any substance or factor which can lead to increased growth rates as its availability in the environment is increased, and which is consumed by an organism" (Tilman, 1982). This definition implies resources that are food items, but if one takes the general definition of "consumed" to mean "used up", then patches of habitat (i.e., space) can also be considered resources. As the dynamics of resources change (e.g., number of available food items, size of patches, the separation of patches in space and time, density of items within patches), the ways in which species within a community assemble and interact will also change on both temporal and spatial scales (Brown, 1989; Belyea and Lancaster, 1999; Fleagle, 1999; Tokeshi, 1999).

Temporal distribution. The temporal or seasonal distribution of resources greatly influences community dynamics. Animal species must be at least somewhat flexible in their dietary preferences, because preferred foods within the environment can increase or decrease over time. This applies to all animal species whether they are mainly folivorous (as leaves mature at different rates), frugivorous (as some plants fruit only every other year or after several years as mast crops), or insectivorous (as insect population densities are tied to variations in resource abundance); for omnivorous animals that eat a combination of leaves, fruits, and/or insects, it becomes even more important to be adaptable to a changing dietary environment. In times of preferred food scarcity, many species will not only change the composition of their diets, but will also alter foraging behavior by either ranging further or staying in core areas around resources. In addition, many species exhibit a change in grouping patterns, with larger groups occurring during times of food abundance and smaller groups occurring during times of food scarcity (Oates, 1987; Gupta and Chivers, 1999; Janson and Chapman, 1999; Strier, 2003). For example, chimpanzees and other primates have been observed to spend more time feeding on lower-quality food items during times of scarcity, and to decrease the mean number of individuals within a foraging party during these times (Oates, 1987; Doran, 1997). Foraging activities, ranging behaviors, and dietary preferences of primates have also been shown to change in response to the presence of fires (whether man-made or natural), which can be seasonal events, particularly in drier woodland or savanna environments (Berenstain, 1986; Tutin et al., 1997; Vilela and Faria, 2004; Galat-Luong and Galat, 2005; Pruetz and Bertolani, 2009).

While the responses of species to seasonality may greatly differ within and between habitats, it is clear that temporal variation has an overall effect on community dynamics. Without seasonal variation in resource availability, there would be less of a need for species to alter their behaviors, and therefore decrease the potential for niche differentiation, which allows multiple species to coexist in the same environment (Giller, 1984; Martin, 1988; Brown, 1989; Wahungu, 1998; Stevenson et al., 2000; Marshall et al., 2009). Furthermore, the degree of seasonality can affect the species diversity and biomass of a community. For example, it is believed that a less seasonal habitat may have more availability of different food types, which would support a greater diversity of primate species, and hence higher biomass, as compared with a seasonal habitat (Gupta and Chivers, 1999).

Spatial distribution. Variability in the spatial distribution of resources, or the existence of patches, in an environment also greatly affects community dynamics. The group size of a species is considerably influenced by the size of patches, as this variable places physical limits on the number of individuals that can be together at the same time. In primates, species that rely on foods that are found in small, evenly scattered patches tend to live in small groups, while species that specialize on foods that are found in large but unevenly scattered patches tend to live in large groups (Fleagle, 1999). The density and quality of food items within a patch also influences group dynamics. Groups tend to be larger when food is abundant because the amount of additional travel imposed by extra individuals is reduced (Wrangham et al., 1996). In general, high-quality foods like fruits have patchier distributions than low-quality foods like leaves. Therefore, primates who are mainly frugivorous, like chimpanzees, tend to forage in smaller groups as compared to folivores, like howler monkeys, that are able to forage in large groups.

Other behaviors, such as territoriality and ranging preferences, are not only affected by the size of patches, but also the distance between resources. Since terrestrial species usually encounter more space between patches, they tend to have longer daily path lengths and larger annual home ranges than arboreal ones. Similarly, frugivores tend to follow longer paths and have larger annual ranges than folivores, as fruits are generally more patchily distributed than leaves (Oates, 1987). If preferred resources occur at high densities relative to an individual's daily travel path, and are within an area that can be economically defended, territoriality will evolve. However, if preferred patches are too small and dispersed to monitor daily, then territoriality is not a viable option (Oates, 1987; Strier, 2003).

WHAT IS A COMMUNITY?

OPEN AND CLOSED COMMUNITIES

The concept of the ecological community has been around for over a century, first depicted in the late 1800's by researchers such as Stephen A. Forbes in his studies on aquatic plant communities, and Karl Mobius' studies of the biotic communities of oyster banks (Southwood, 1986; Ricklefs, 1990). Both researchers noted that groups of coexisting organisms were possibly functioning together as a unit, and this observation led to questions about the composition and structure of these units, or communities. Early attempts to answer such questions resulted in two major views regarding how processes controlled the structure of communities: closed versus open concepts.

Proponents of the closed community concept, such as F.E. Clements, V.E. Shelford, and C. Elton, argued that communities consist of closely interlinked species that interact with each other and their environment, which is a closed unit with sharp boundaries. In other words, the environment constrains the animal members of the community, and is isolated, with no immigration or emigration (Elton, 1927; Shelford, 1931; Clements, 1936; McIntosh, 1980; Southwood, 1986; Leibold et al., 2004; Reed and Bidner, 2004). In contrast, the concept of an open community shifts the focus from location (i.e., the environment) to that of composition, suggesting that the immigration and emigration of species, in addition to the adaptations and interactions of species, are what determines the structure and function of community (Gleason, 1926, 1939; Southwood, 1986; Leibold et al., 2004; Reed and Bidner, 2004). In reality, it is more probable that community boundaries occur on a continuum from closed to open.

More recently, communities have been described in terms of species interactions on a finer level. Communities in which strong interactions (e.g., competition, predation, mutualism) take place among species at the same trophic level are deemed interactive, while a non-interactive community has weak or absent local (i.e., within trophic level) interactions. Therefore, local processes play a key role in structuring species assemblages in interactive communities, while non-interactive communities are mostly influenced by the history of colonization from the surrounding area (Cornell and Lawton, 1992). Realistically, communities more likely fall along a continuum between interactive and non-interactive.

There is much debate among researchers regarding the definition of a community and the processes that shape community composition and organization, but most would probably agree that a community can generally be defined as an assemblage of organisms that co-exist, interact with one another, and use resources accessible in the same temporal and spatial region.

COMMUNITY FEATURES

Species diversity and richness. The terms “species diversity” and “species richness” are commonly used interchangeably to mean the number of species present in a community, but more often “species diversity” also reflects the abundance and distribution (i.e., evenness) of species (Whittaker, 1977; Connell, 1978; Krebs, 1999). There are generally three types of species diversity found in ecological research: α-, β-, and γ-diversity. α-diversity is the diversity of species within a habitat or community, β-diversity measures the differences between species from one habitat to another along an environmental gradient, and γ-diversity describes the diversity of species in a range of communities in a location or from one location to another on a geographical scale (Bourliere, 1983; Southwood, 1986; Tokeshi, 1999). In other words, the scale at which diversity is measured increases from within a community to between communities to among regions as one goes from α- to β- to γ-diversity.

Measures of diversity and richness. There are numerous ways to measure the diversity and richness of a community, the simplest method being a basic count of the number of species found. High numbers of species would indicate high richness and low numbers would indicate low richness. However, this measure of richness is only a relative measurement and can only be used to compare communities if sample sizes of animal species present are equal. Further, as this measure does not take into account the frequency of each species, it does not give a true measure of diversity as described above, which reflects the abundance and distribution of species. Thus, various indices have been developed so that relative diversity and richness of species in a variety of communities could be compared.

One commonly used index is Simpson's Diversity Index, which gives higher values for greater diversity based on the proportions of species within a community. A similar index that was based on the Simpson Index is the GINI Index, which is calculated based on the density of each species within a community in relation to the total number of species present. When using the GINI Index, uncommon species will contribute less to the final sum than species with greater frequencies. Therefore, these two indices can also be called dominance measures, as they reflect the degree of dominance of the most common species in the community (for formulas, see Legendre and Legendre, 1998; Krebs, 1999; Zar, 1999).

Other indices measure the distribution or evenness of species based on their densities, such as the McIntosh Evenness Index; the higher the value for evenness, the more equal or uniform the distribution of species (formula in: Legendre and Legendre, 1998; Reed 1999). Which index is used in a study, whether one listed above or another (e.g., Richness Index, Shannon Diversity Index), will be determined by the research question being asked and the nature of the data. For example, Simpson's index places more importance on the common species, as compared to Shannon's index, which gives the rare species more weight; therefore, Shannon's index is likely to underestimate species diversity, particularly for small sample sizes (Lande, 1996; Smith and Wilson, 1996: Hubalek, 2000; Stirling and Wilsey, 2001).

These indices are important because they allow the quantification and standardization of key features of community composition and structure. More specifically, these indices provide information about rarity and commonness of species in a community. These factors greatly influence the dynamics of species interactions, including how species utilize and share resources and space. Therefore, the seemingly basic measures of species diversity and richness (through indices) are crucial baseline characteristics for any study of community ecology, particularly one that is focusing on ecological partitioning of space and resources.

General patterns of diversity and richness. There are some common patterns of species diversity and richness that hold for most animal communities across the globe. As areas get larger, there is a general increase in available space, and thus the potential for an increase in habitat heterogeneity. However, if spatial complexity does not change, and there is simply an increase in available space, it is likely that the number of species will remain the same, but that population sizes of each species will increase (Cowlishaw and Dunbar 2000). If there is an increase in habitat complexity, then diversity is expected to increase, possibly because habitat heterogeneity provides more available ecological niches, thus allowing more species to coexist. In this respect, forested habitats, which are more floristically complex, typically have more animal species than woodland or savanna habitats (Bourliere, 1983, Cowlishaw and Dunbar, 2000).

Other biogeographical patterns include those related to latitude and altitude. In general, species richness decreases with increasing distance from the equator and with increasing altitude. This pattern has been shown in a variety of taxa including mammals, primates, birds, some terrestrial invertebrates, and even some plant species. This pattern is thought to result from lower temperatures, smaller areas with less habitat heterogeneity, and increased isolation of habitats at higher altitudes (Eeley and Lawes, 1999; Tokeshi, 1999).

INTERSPECIFIC INTERACTIONS

Interactions between animal species of a community can greatly influence the structure of that community. These interactions range from mutualism or cooperation (positive, favoring both species) to predation or unbalanced cooperation (one species benefits more than the other) to direct competition (negative, both species inhibited). Species interactions can also be neutral, wherein neither species significantly impacts the other. Table 2-1 lists the possible interactions of two species, which will be discussed in more detail below.

Table 2.1
Potential population interactions of two species (from Richard, 1985)

Type of interaction	Species* A	B	Nature of interaction
1. Neutralism	0	0	Neither population affects the other
2. Mutualism	+	+	Interaction favorable to both and obligatory
3. Protocooperation	+	+	Interaction favorable to both but not obligatory
4. Commensalism	+	0	Population A, the commensal, benefits while B, the host is not affected
5. Parasitism	+	-	Population A, the parasite, exploits B, the host
6. Predation	+	-	Population A, the predator, kills and eats B, the prey
7. Amensalism	-	0	Population A inhibited, B not affected
8. Competition	-	-	Each population inhibits the other

*0: not affected; -: negatively affected; +: positively affected

Neutralism. Neutral associations between two or more species are those that result in the absence of net benefits or negative inhibitions to either species. In fact, most interspecific interactions in the wild are neutral or passive. These interactions are generally characterized by tolerant spatial proximity resulting from a shared interest in resources, including food items and habitat space. In communities where population densities are high it is even more likely for groups to come in contact with each other and exhibit such tolerant behaviors (Waser, 1987; Asensio et al., 2007). While the species involved do not have direct physical contact, these interactions are nonetheless important for examining the organization of a community and in determining how resources are shared between community members. Additionally, neutral behaviors could possibly be the result of past adaptations, and so could provide some insight into the evolutionary history of the community.

Mutualism/Cooperation/Commensalism. Mutualism and cooperation are interactions that provide net benefits to both species involved. Commensalism results in benefits for one species, but does not negatively impact the second species, so it is considered to be a positive association like mutualism and cooperation. A common example of commensalism is the relationship between cattle egrets and livestock. Cattle egrets feed on the insects that are stirred up by the movement of the grazing animals; however, some of these birds have also been known to pick ticks off cattle, which would be more of a mutualistic relationship. Cooperation seems to be more frequent between taxonomically distant species with dissimilar body sizes and may be a significant process by which organisms have acquired new traits and invaded niche spaces, which were not previously available (Tokeshi, 1999). However, cooperation also occurs between closely related species, or species that fill similar ecological niches. For example, Do Linh San and Somers (2006) observed cooperative vigilance between one yellow mongoose and three meerkats while the animals were travelling from one termite mound to another.

The most cited instances of mutualism in the wild occur in polyspecific associations, where individuals of different species aggregate together. It is important to note that there are also potential costs to such associations, so mutualism and/or cooperation might not be the only interaction present, but it is the one that receives the most focus. It is thought that potential benefits of mixed-species groups include: access to otherwise unavailable food (e.g., dropped fruit, flushed prey, location of new fruit/leaves), more effective foraging, a competitive advantage compared to a smaller monospecific group, enhanced predator protection, and social benefits such as playing and grooming (Terborgh, 1983; Richard, 1985; Waser, 1987; Chapman and Chapman, 1996; Cowlishaw and Dunbar, 2000; Strier, 2003; Haugaasen and Peres, 2008).

Polyspecific associations are very common among primates, particularly within the cercopithicines and the callitrichids. Primates have also been observed in association with birds (e.g., tamarins and woodcreepers, Hankerson et al., 2006; kestrels and baboons, King and Cowlishaw, 2009) and other mammals (e.g., macaques and deer, Majolo and Ventura, 2004; howlers and coatis, Asensio et al., 2007; squirrel monkeys and coatis, Haugaasen and Peres, 2008). Therefore, mutualistic and cooperative behaviors are integral to the study of any primate community.

Predation. Predation is an interaction between two species in which one preys upon (i.e., kills and eats) another. Predator-prey relationships are perhaps one of the most studied interactions among animal communities, along with competition, as predation patterns immensely affect population dynamics, and therefore community structure. In theory, over time predation may eliminate certain prey species and encourage evolution of others, thus changing the composition of coexisting species. However, predators more realistically cause a decline in one prey species and then switch to another species (or have multiple simultaneous prey species), which prevents the complete extinction of its prey. Therefore, predation has a greater impact on the density of species populations. Effects of predation are more influential on community structure when it is concentrated among animals of high reproductive value, such as juvenile and young reproductive females (as compared to infants and males). In essence, predation can increase overall species richness or maintain it at a high level if predators preferentially feed on more abundant or competitively dominant prey species (Southwood, 1986; Cheney and Wrangham, 1987; Tokeshi, 1999).

Predation has also influenced many morphological and behavioral traits of prey species, which in turn affect interspecific interactions between differing prey species, and between prey and predator species. Strong selection pressure by predation is well exhibited in the behavior of most birds and mammals that give alarm calls to predators, with many species even appearing to have different calls for specific types of predators (Parrish and Saila, 1970; Cheney and Wrangham, 1987; Isbell, 1994; Rainey et al., 2004; Isbell, 2006).

Direct predation events are often difficult, if not near-impossible, to observe in the wild, so researchers must look for clues of predation pressure, such as the presence of anti-predator behaviors (such characteristics would have not been selected for in the evolutionary past if they were not adaptive) and rates of population decline that cannot be explained by other factors (e.g., disease, emigration, etc.). However, as primates are prey to many larger mammals (including other primates such as chimpanzees) and birds, predator-prey relationships, no matter how complex or difficult to observe, are an important variable in determining composition and structure of primate communities.

Competition. Competition (currently occurring and in the past) between species has long been perceived as an important determinant of community structure (e.g. Connell, 1983; Schoener, 1983; Stevenson et al., 2000), and thus is a very prevalent research topic in the ecological literature. For this discussion, amensalism is subsumed into competition as it is not widely used by practicing ecologists, and many competitive relations occur in an asymmetric manner (Tokeshi, 1999).

Traditionally, interspecific competition is divided into two classes of mechanisms, exploitative and interference. In exploitative competition, individuals deprive others of benefits to be gained from resources by using those resources first. Interference competition is more direct, with individuals aggressively excluding another from the resource. Interference competition may be the result of either contest or scramble competition; contest competition results in the complete use of a resource by one competitor, while all competitors try to utilize the same resource as much as possible during scramble competition (Rohde, 2006). Habitat space, like any resource, can be used or modified to deprive others of its benefits, but most cases of competition for space involve direct interference (Schoener, 1983; Waser, 1987; Tokeshi, 1999; Passarge and Huisman, 2002). As competition influences behavioral and morphological adaptations, and therefore niche spaces, of animals, it can be correlated to other aspects of community structure and composition. However, these correlations are not always straightforward. For example, competition for one or two limiting factors is generally associated with low species diversity, but increasing the number of limiting resources available can both increase or decrease amounts of competition depending upon particular species' niches (Passarge and Huisman, 2002). Increasing resources could make more niche space available thus relaxing competition pressure. However, if multiple species are trying to simultaneously fill these new niche spaces (i.e., utilize more resources), increased competition between the species will occur.

In the absence of direct observation of competitive interactions, there are other indicators one can use, particularly in an experimental setting. For example, an increase in one species' population density or a shift in niche space when a competitor is absent indicates competition. Similarities in resource use can also be interpreted as indicating that species compete, as it is thought that no two species can occupy the same niche space (see niche concept and competitive exclusion principle below for further discussion) (Waser, 1987). Using similarities in resource use (i.e., the amount of overlap in use) between species is not always a good proxy for competition, particularly because there is no agreement among ecologists as to the amount of similarity in resource use required for species to undergo pressure to compete. However, in a natural setting with wild populations it is difficult to observe and/or measure increases in population density on a short-term scale. Therefore, many field researchers rely heavily upon the amount of overlap in resource use between species to approximate levels of dietary and/or spatial competition.

An apparent lack of competition between species in present day communities does not reflect on the importance of competition in shaping those communities in the past. Therefore, it becomes important to distinguish current competition from past competitive effects, although this distinction is largely ignored in the literature and in most ecological studies (but see Connell, 1980). The main difference between contemporary competitive effects and evolutionary competitive effects is the scales at which they operate. Current competition occurs at the individual level, with individuals of the same or differing species. In contrast, past competition operated at the population level (again, within a single species or between species). Both levels of competition greatly influence the types, abundance, and distribution of species within an assemblage. Species interactions in present communities must therefore be examined within both contemporary and evolutionary contexts to fully understand community dynamics. This is not an easy task, as there seems to be no linear correlation between past and present competition (e.g., a lack of current competition need not necessarily reflect large amounts of past competition), but nonetheless a crucial variable in any community ecology study.

COEXISTENCE OF SPECIES

COMPETITIVE EXCLUSION PRINCIPLE

One of the earliest ecological theories tying together competition and the coexistence of species was put forth by Gause (1934) who proposed that two species that compete for the same limiting resources cannot coexist in the same place at the same time. Thus, the competitively superior species will exclude the other species to the point of its extinction (Hardin, 1960; Jaeger, 1974; Campbell and Reece, 2001). This "competitive exclusion principle" has received much criticism since its inception in ecology, mainly due to its many underlying assumptions that are unrealistic. The principle assumes that: 1) population growth rate is unaffected by that population's density; 2) individuals in the competing populations have identical demographic characteristics; 3) there are no random effects or time lags in the interactions between the populations; 4) there is spatial and temporal homogeneity of the populations' environments; 5) the interactions between species are directly affected by only a single limiting resource, which is of uniform quality; and 6) no evolutionary or behavioral changes occur in either species (Richard, 1985). Most, if not all, of these assumptions are violated by natural communities, which are generally located in temporally and spatially heterogeneous environments with variable numbers of limiting resources that fluctuate over time. Furthermore, it is unlikely that a species will be driven to extinction; instead, there is often a shift or change in one or more characteristics of one or both species to release competition pressure (see “niche overlap” below). While the competitive exclusion principle might not be a realistic phenomenon of communities, it has greatly influenced the research of species coexistence, particularly that of the niche concept (Giller, 1984), so it should not be completely overlooked as an important ecological concept.

NICHES AND ECOLOGICAL ROLES

The concept of a niche was first introduced by Grinnell (1917a, b) as the place in the environment that an organism occupies (i.e., a habitat concept). In contrast, Elton (1927) focused on the functional concept of niche, describing it as an organism’s place in the biotic environment in terms of its role within the food chain and its impact on the environment, (Giller, 1984; Chase and Leibold, 2003). Ultimately, these habitat and functional concepts were combined to form perhaps the most commonly cited niche concept given by Hutchinson (1957) who defined a niche as a multidimensional hypervolume in which a species can maintain a viable population. This hypervolume is characterized by both abiotic and biotic factors that cover the total range of environmental variables to which a species must be adapted (Giller, 1984; Richard, 1985; Campbell and Reece, 2001). Tokeshi (1999) expanded upon this definition and noted that the hypervolume may take any shape and size, that any particular niche of a species may change over ecological and evolutionary time, and that the niches of different species may overlap partly, but never completely. This last concept of partial niche overlap correlates with the division of niche into two types: fundamental and realized.

Fundamental versus realized niche. In his definition of niche, Hutchinson (1957) made the further distinction between fundamental and realized niches. He defined the fundamental niche as the total range of conditions under which a species can exist. Defined in this way, a fundamental niche can also be described as a potential niche, consisting of all the possible realized niches a species does or could inhabit. "If [a species'] niche overlaps with that of another species…then the area of overlap is either incorporated into the niche of one species and the other becomes extinct, or else the area is divided between the two, producing the realized niche of each" (Richard, 1985, p. 388). Therefore, the realized niche of a species results after one or both species go through an ecological shift, and describes the actual set of conditions in which a species normally exists (Giller, 1984; Chase and Leibold, 2003).

Ecological role. This dissertation uses the term "ecological role" synonymously with "niche" to emphasize the main focus of this project: to determine what space, or role, chimpanzees occupy within their larger faunal communities and environments.

NICHE OVERLAP

Most organisms inhabit their realized niches, which, as described above, can be viewed as a subset of their potential or fundamental niche. Therefore, species tend to share parts of each other's fundamental niches, resulting in simultaneous demands upon some resource by two or more species populations. Figure 2-2 shows the possible relationships between species' niches, ranging from complete overlap to complete disjunction. If niche overlap is small, or resources are superabundant, then species can coexist in essentially separate and almost fundamental niches (Figure 2-2c,d). If niches overlap to a greater extent, and resources are scarce, then the abundance of the less-efficient species will be limited by its interactions with the more efficient species (Figure 2-2a,b; Giller, 1984). This overlap in niche space can be related to the competitive exclusion principle described above, if the principle is reworded to state that no two species occupying the same niche can coexist. While the extreme outcome of the competitive exclusion principle (i.e., extinction) is not likely to occur in natural communities, quantifying degrees of niche overlap and determining patterns of how species differentiate niche space to reduce this overlap can give insight into community structure, particularly species coexistence.

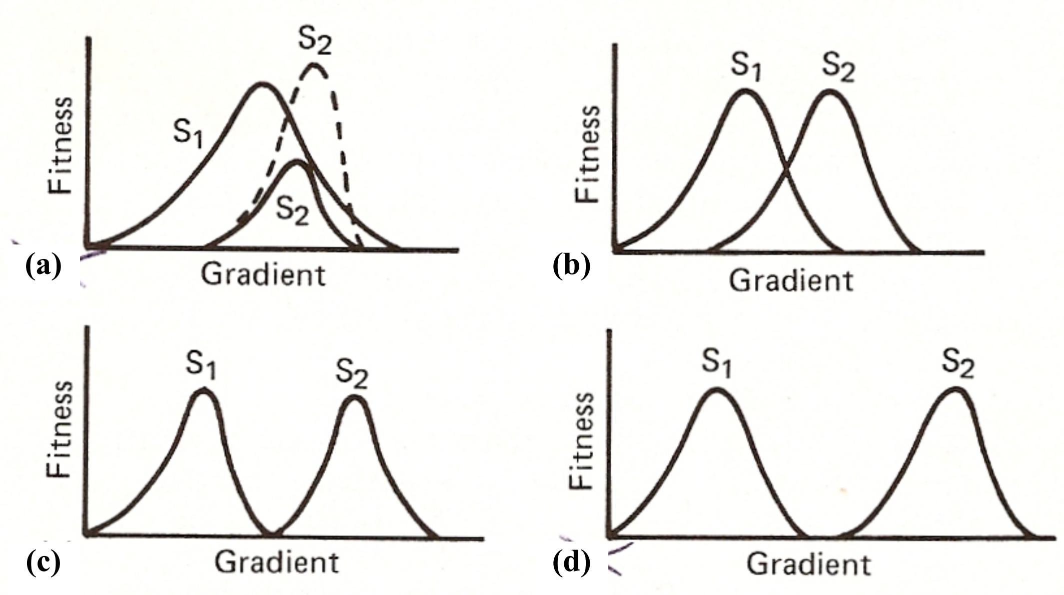


Figure 2-2. Possible niche relationships between two species on a single environmental gradient. (a) One fundamental niche totally included within larger one; (b) Partial overlap of niches; (c) Abutting niches; (d) Disjunct niches, both species occupy fundamental niche (from Giller, 1984).

NICHE DIFFERENTIATION

As niche defines the total ecological space a species occupies, niche differentiation can occur on many levels (i.e., any of the dimensions in the niche hypervolume). The best-understood and most cited type of niche differentiation is resource partitioning, which generally refers to the state of reduced overlap in resource use between coexisting species. Schoener (1974) found that partitioning occurred most frequently along the habitat axis, followed by the food axis, while temporal partitioning was rare. These results are not surprising, given that habitats can be divided into a large range of spatial scales (e.g., soil patches, tree patches, forest patches, landscapes, vertical strata, etc.), while food and temporal partitioning do not have as many subcategories. Further, while partitioning in the food or time axis leads almost directly to a reduction in the overall level of energy intake, habitat partitioning does not. Therefore, habitat partitioning would be more adaptive in terms of species fitness (Tokeshi, 1999).

Partitioning strategies are often correlated with one another and very rarely occur in isolation of other strategies. Further, partitioning of niche space occurs both between species and within species. Spatial partitioning can occur vertically, horizontally, or via differing patch sizes. Temporal separation can take place daily (i.e., diurnal versus nocturnal species) or seasonally, in which foraging and other social behaviors most often change during periods of fruit scarcity with species turning to “fall-back” foods. Behavioral strategies include different social organizations, such as fission-fusion that is believed to enhance foraging efficiency; an increase in the distance traveled to food patches; and use of technology to acquire resources that others cannot utilize (e.g., use of tools by orangutans to extract seeds from *Neesia* fruits: Fox et al, 1999). Morphological differences between species (or intraspecific differences such as sexual dimorphism) also influence how species partition niche space.

Perhaps the most common niche separation strategy is that of dietary partitioning. This includes species eating different food types (e.g., leaves versus fruits), eating different species of the same food type, or eating various parts of the same species (e.g., mature versus immature leaves). The diet of a particular species is greatly influenced by the availability and distribution of resources, so species often utilize "resource switching" and fall back on less desirable or lower quality foods when preferred foods are seasonally scarce (Charles-Dominique, 1974; Struhsaker, 1981; Oates, 1987; Overdorff, 1993; Singh et al, 2000; Stevenson et al, 2000; Lambert, 2002). Resource switching specifically provides a means to minimize intra- and interspecific contest competition, as a flexible dietary strategy means that more items are considered food, which ultimately decreases the likelihood of encroaching on another individual's feeding space (Lambert 2002).

As ecological pressures vary between and within species, the particular niche partitioning strategies utilized by a species will depend upon the context in which it finds itself. If the community structure changes, the available niche spaces will also change, so we would expect to see various behavioral responses to these shifting niches. It is possible that species with highly constrained or inflexible niches need to have greater intraspecific partitioning to avoid within-group competition, while ecologically flexible species can occupy a larger niche space and are thus under relaxed pressures with no need to partition intraspecifically (Cowlishaw and Dunbar, 2000; Strier, 2003). However, the niche space available to a species is limited by the presence of other species and their niche requirements, which will influence how flexible a species can be.

SUMMARY OF COMMUNITY ECOLOGY

Almost a century after the concept of community first appeared in the literature its definition is still debated among researchers, but despite this lack of agreement, there are a number of key components of plant and animal communities that are examined in any community ecology study. Habitat structure and heterogeneity greatly influence resource distribution in time and space, which in turn impacts the types, abundances, and distributions of plant and animal species within those habitats. The way in which species divide their space and resources (i.e., patterns of resource use and niche differentiation) and the kinds and frequencies of interspecific interactions provide insight into how these communities function and adapt to changing variables. The following sections describe these important components for chimpanzee communities.

CHIMPANZEE COMMUNITY ECOLOGY

CHIMPANZEE HABITATS

Currently there are four recognized subspecies of the common chimpanzee, *Pan troglodytes*: the central (*P. t. troglodytes* Blumenbach, 1799), the western (*P. t. verus* Schwarz, 1934), the eastern (*P. t. schweinfurthii* Giglioli, 1872), and the Nigeria-Cameroon (*P. t. ellioti* Gray, 1862) chimpanzee (Gonder et al., 1997; Inskipp, 2005; Stumpf, 2007; Oates et al., 2008; Bowden et al., 2012). Chimpanzees live in a wide variety of habitats, including (but not limited to) humid evergreen forest, deciduous forest, and dry savanna woodlands. Their distribution covers 21 countries across Africa and a range of elevations from sea level in West Africa to 2600m in East Africa (Figure 2-3; Richard, 1985; Caldecott, 2005; Inskipp, 2005; Russak and McGrew, 2008).

Studies of chimpanzees have sampled many communities throughout this distribution (Table 2-2). As many sites are mosaic environments, each site provides chimpanzees with varying ecological conditions (e.g., vegetative structure, fruit availability, moisture, etc.) and therefore, chimpanzees utilize habitat patches differently. My research specifically addresses the impacts of living in a dry, open environment on chimpanzee behaviors.

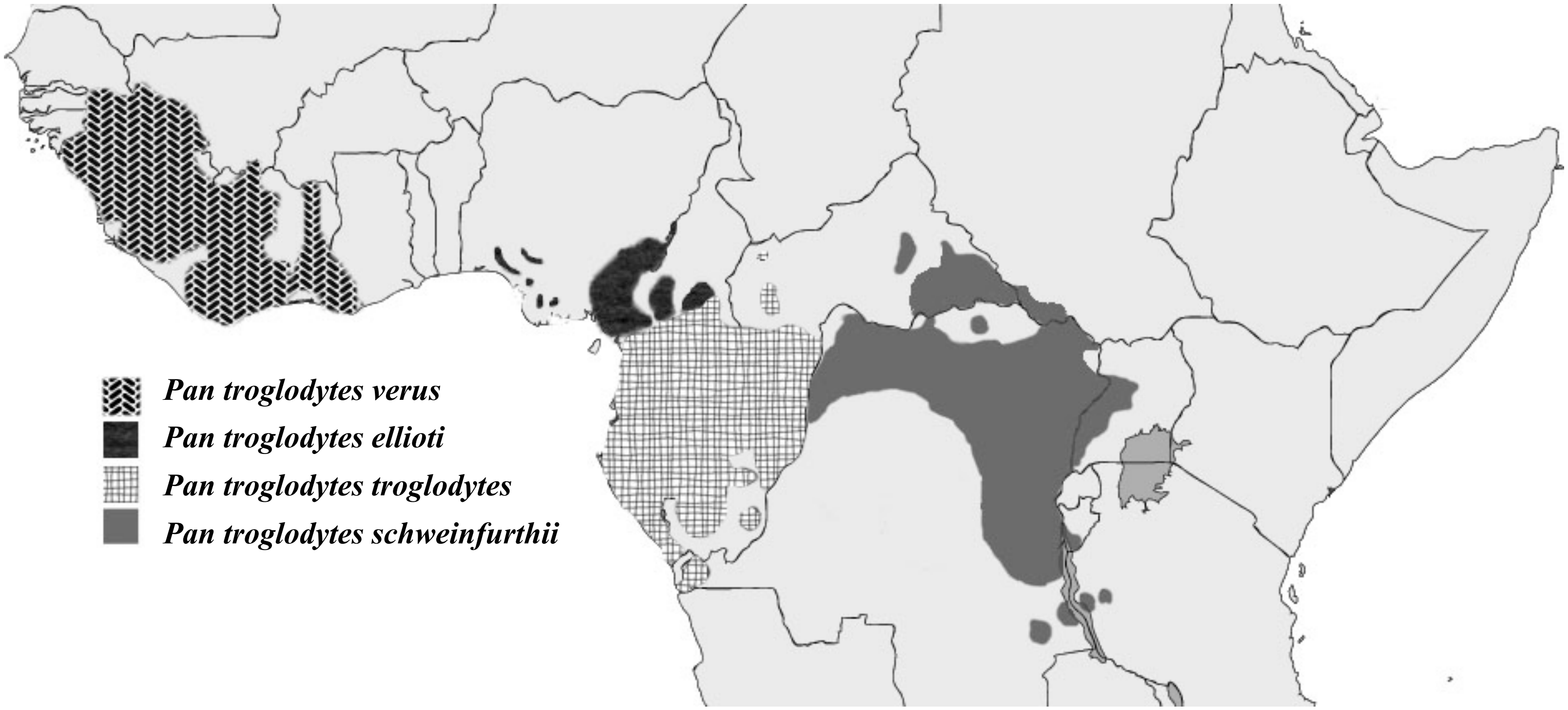


Figure 2-3. Distribution map of the four chimpanzee subspecies.

Table 2-2

Main chimpanzee study sites and locations (adapted from Inskipp, 2005 and Stumpf, 2007)

Site	Country	Subspecies	Major References
Bafing	Mali	western	Kortlandt, 1983
Bossou	Guinea	western	Sugiyama, 2003
Budongo FR	Uganda	eastern	Reynolds, 1992
Bwindi Impenetrable NP	Uganda	eastern	Butynski, 1984
Dzanga-Ndoki NP	CAR	central	Blom et al., 2001
Fongoli	Senegal	western	Pruetz et al., 2002
Gashaka Gumti NP	Nigeria	N-C	Sommer et al., 2004
Gombe NP	Tanzania	eastern	Goodall, 1986
Goualougo Triangle, Nouabale-Ndoki NP	Congo	central	Morgan & Sanz, 2003
Ishasha River	DRC	eastern	Schoeninger et al., 1999
Ituri FR	DRC	eastern	Hart & Thomas, 1986
Kahuzi-Biega NP	DRC	eastern	Hall et al., 1998
Kalinzu FR	Uganda	eastern	Hashimoto, 1998
Kasakati	Tanzania	eastern	Izawa & Itani, 1966
Kibale NP	Uganda	eastern	Ghiglieri, 1984
Lope NP	Gabon	central	Tutin et al., 1997
Mahale Mountains NP	Tanzania	eastern	Nishida, 1990
Minkebe NP	Gabon	central	Huijbregts et al., 2003
Monte Alen NP	Equatorial Guinea	central	Garcia & Mba, 1997
Mount Assirik, Nikolo-Koba NP	Senegal	western	Baldwin, 1979; Baldwin et al., 1982
Ngotto Forest	CAR	central	Hicks et al., 2005
Nimba Mountains	Guinea	western	Matsuzawa & Yamakoshi, 1995
Nouabale-Ndoki NP	Congo	central	Kuroda et al., 1996
Odzala NP	Congo	central	Bermejo, 1999
Semliki-Toro WR	Uganda	eastern	Hunt, 2000
Tai NP	Cote d'Ivoire	western	Boesch & Boesch, 1989
Tenkere	Sierra Leone	western	Hanson-Alp et al., 2003
Tongo, Virunga NP	DRC	eastern	Lanjouw, 2002
Ugalla	Tanzania	eastern	Nishida, 1989

NP: National Park, N-C: Nigeria-Cameroon subspecies, FR: Forest Reserve, WR: Wildlife Reserve

IMPORTANT FOOD RESOURCES FOR CHIMPANZEES

Despite their extremely widespread distribution across habitat types, chimpanzees have been found to eat *generally* the same food items. They are classified as ripe-fruit specialists that also eat leaves, flowers, seeds, a variety of small mammals and invertebrates, and various other food items like algae, mushrooms, and honey when available (Richard, 1985; Cowlishaw and Dunbar, 2000; Caldecott, 2005; Inskipp, 2005). Table 2-3 shows a general dietary profile of chimpanzees resulting from a compilation of various studies at particular sites; more specific details about chimpanzee diet, and its diversity across sites, is discussed further in Chapter 8.

It is clear that while chimpanzee diets across sites are generally similar, each study site, and even specific communities within those sites, has a particular dietary profile, which can be only partly explained by environmental differences. Therefore, it is important for researchers to continue to get detailed habitat and dietary information for each chimpanzee community studied so that the variability (and similarity) of chimpanzee diets can be adequately examined and explained within an ecological context.

Table 2-3
General dietary composition of chimpanzees (from Stumpf, 2007)

	(%) of diet	**Range (%)**
Fruit	64	19—99
Leaves	16	0—56
Terrestrial Herbaceous Vegetation	7	0—27
Bark and Misc.	4	0—41
Prey	4	0—28
Flowers	2	0—14
Seeds	3	0—30

Links between resources and chimpanzee behavior. Habitat type, and thus availability and distribution of resources, can greatly influence behavioral characteristics of chimpanzees. Perhaps the most obvious connection between habitat and behavior is that of foraging strategies and dietary preferences. Many studies have found that in times of fruit scarcity chimpanzees will increase the proportion of leaves and low-quality foods in their diets, although the amount of increase varies across sites (Wrangham et al., 1998; Strier, 2003; Yamagiwa and Basabose, 2006). Most differences of the quantity and types of mammalian and insect species eaten can also be explained in terms of environmental influences, such as the presence or absence of prey species, range of potential prey species (which is influenced by habitat characteristics), and presence of competing predators. However, it is important to note that such environmental factors do not explain *all* dietary variation, so cultural behavior (see below) must be considered as well (McGrew, 1983).

Closely tied to the distribution of food resources is social organization. Female chimpanzees in particular are limited by the abundance and availability of food. Therefore, grouping patterns are affected by seasonal fluctuations in the size of fruit patches. In general, most females travel in small parties or alone to forage, especially when foods are very patchily distributed (Strier, 2003). The distribution of females within an area, in turn, affects the grouping patterns of male chimpanzees, particularly when females are in estrous. Therefore, food distribution can be correlated to total party size (Mitani et al., 2002).

In addition to feeding behaviors, cultural traditions of chimpanzees are also closely linked to the environment. Behaviors that are deemed cultural are those that vary across sites, but cannot be explained by differences in environmental variables (Strier, 2003; Inskipp, 2005). For example, researchers would expect to find chimpanzees using hammer and anvil stones to crack nuts wherever nuts and stones were available in the same habitat. However, one population of chimpanzees in the Lope Reserve, Gabon does not crack nuts even though all of the raw materials are available and nuts are highly desirable food to other chimpanzee populations (McGrew et al., 1997). Therefore, it seems that this is a cultural difference, likely due to a lack of knowledge of the technology. There are many other behaviors that show similar patterns; they are absent at some sites even though they are expected to be there. Many researchers (Boesch and Boesch, 1990; McGrew et al., 1997; Sugiyama, 1997; Boesch and Tomasello, 1998; Whiten et al., 1999; Whiten and Boesch, 2001; Whiten et al., 2003; McGrew, 2004) provide extensive reviews of cultural patterns of chimpanzees, and how these behaviors relate to, or are independent of, the environment.

While many behavioral differences cannot be explained by environmental variables, others can. For example, chimpanzees in areas of water scarcity have been observed to chew on rotten wood, use leaf sponges, or even dig wells to find water (Hunt and McGrew, 2002; Lanjouw, 2002; Quiatt, 2006). Other “environmentally explicable” behaviors include the abundance of ground night-nests (due to lack of tall sturdy vegetation), the use of anvil props, and scooping algae (Whiten et al., 2001).

Community ecology studies that examine environmental variables, animal behavior, and how those factors are correlated can provide insight into how animals are adapted to and manipulate their environment in order to be evolutionarily successful. This is particularly important for chimpanzees, because they are ecological generalists occurring in a wide range of habitats that present numerous combinations of environmental variables. Examining and comparing communities will lead to a better understanding of how chimpanzees utilize and survive in so many habitats (and perhaps why other large primates, like bonobos and gorillas, do not), and how differences in behavior relate to differences in habitats. Understanding these relationships has important research implications for the fields of conservation and human evolution, which are discussed more in detail below.

SPECIES SYMPATRIC WITH CHIMPANZEES

As expected from their wide distribution, chimpanzees are sympatric with a large diversity of other fauna, with each community having a unique combination of species present. For example, Russak and McGrew (2008) found a low overlap of mammalian taxa between six long-term study sites, reflecting the large diversity of mammalian communities that co-occur with these apes.

Chimpanzees are found with species from numerous taxonomic groups including ungulates (e.g., kob, bushbuck, waterbuck, reedbuck), felids (e.g., leopard, lion), suids (e.g., warthog, forest hog), other primates (e.g., gorillas, redtail monkeys, baboons, blue monkeys), and many others. The specific types of individual species sympatric with chimpanzees are too numerous to mention, but the following sources provide this information. For lists of sites where chimpanzees are sympatric with gorillas: Kuroda et al. (1996) and Stanford (2006); mammal species present at the sites of Mt. Assirik, Gombe, Mahale, Tai, Kibale, and Budongo are given in Tables I-V in Russak and McGrew (2008); some of the sympatric species at Semliki, Uganda are given in Hunt and McGrew (2002); Ogawa et al., (2007) lists primates and large mammals in Ugalla, Tanzania; and McGrew (1983) presents potential prey and competitors for chimpanzees at Gombe, Kasoje (Mahale), and Mt. Assirik. This list is clearly not exhaustive, but provides some of the more easily accessible references.

Unfortunately, lists of species that are sympatric with chimpanzees are rare among primatological literature. Species lists that can be found are not all-inclusive, and are usually limited to potential prey, competing species and/or particular taxonomic groups, such as mammals. Therefore, it would be useful for future chimpanzee research at various study sites to include faunal lists of sympatric species.

INTERSPECIFIC INTERACTIONS IN CHIMPANZEE COMMUNITIES

The research on interspecific interactions of chimpanzees and other fauna is mostly limited to predator-prey and competitive relationships. Other types of interactions, such as neutralistic or mutualistic occurrences, are rarely reported, and if so, are usually limited to interactions between chimpanzees and other primate species. Comparisons of all types of interspecific interactions across communities are important in identifying behavioral traits that respond to ecological conditions as opposed to being phylogenetically controlled.

Neutralism and mutualism/cooperation/commensalism. Most information on neutral or mutualistic interactions comes from sites where chimpanzees are sympatric with gorillas, as researchers are interested in how two very similar animals, in terms of being large-bodied apes, can coexist in the same area. For example, co-feeding of chimpanzees and gorillas in the same trees has been observed at Ndoki, Congo (Kuroda et al., 1996) and at Goualougo, Republic of Congo (Morgan and Sanz, 2006). In the latter instance, co-feeding was observed in the same tree crown and also in the same tree, but separated by vertical distance, with a solitary silverback gorilla feeding on fallen fruits on the ground while chimpanzees foraged in the canopy. Chimpanzees have also been observed co-feeding with mangabeys (*Lophocebus albigena*) and guenons (*Cercopithecus nictitans*) at Goualougo (Morgan and Sanz, 2006), and with redtail monkeys (*Cercopithecus ascanius*) and black-and-white colobus (*Colobus guereza*) at Semliki, Uganda (personal observation, 2008). Yamagiwa et al. (1996) did not see chimpanzees co-feeding with gorillas in the same trees, but noted that each species of ape tolerated the other's foraging within the same area.

Other interactions between chimpanzees and animals such as servals, duikers, and other primate species have been described as investigative, agonistic or even playful (Teleki, 1973). Goodall (1986) observed juvenile chimpanzees and juvenile baboons playing together at Gombe. While these behaviors do not fall under the categories of predation or competition, it is unclear if they would be considered neutral or mutualistic, as the benefits and costs of play are still debated.

Predation. Predation is one of the most well studied interactions of chimpanzees with other animals. Researchers have examined the role of chimpanzees as prey, as well as the role of chimpanzees as predators of other mammals, particularly other primates.

The major predator of chimpanzees, besides humans, is the leopard (*Panthera pardus*), which occurs at all chimpanzee sites. Boesch (1991) documented interactions between chimpanzees and leopards at Tai, Ivory Coast and found that encounters always appeared to be aggressive and were normally very brief. Encounters were classified into one of three categories: chimpanzees attacking leopards (not very common), leopards attacking adult chimpanzees (mostly females were attacked), and predation on chimpanzees by leopards. The drier, more open sites could also include animals such as lions and hyenas as potential predators. At Mt. Assirik, Senegal (towards the more open extreme of chimpanzee habitats) the major predators of chimpanzees are leopards, lions, hyenas, and wild dogs (Baldwin, 1979).

Much more research has been done on chimpanzee predation of other mammals. Wild chimpanzees at over twelve study sites have been seen to consume and/or hunt at least 32 species of mammals including animals like guenons (*Cercopithecus* spp.), colobines (*Colobus* spp.), baboons (*Papio* spp.), flying squirrels, tree pangolins (*Manis* spp.), duikers (*Cephalophus* spp.), and elephant shrews (Uehara, 1997; Caldecott, 2005). The most studied predator-prey relationship of chimpanzees is between these apes and red colobus monkeys (*Piliocolobus* spp.), which are the favored prey at most sites where these monkeys and apes co-exist (Stanford, 1998; Boesch et al., 2002). However, the particular preference of prey species varies across sites. For example, chimpanzees at Tai and Gombe hunt red colobus most frequently, but at Mahale guenons are hunted more often (Cowlishaw and Dunbar, 2000). In a comparison of these three communities, Uehara (1997) found that blue duikers and bushpigs were popular prey items of Mahale and Gombe chimpanzees, but completely ignored by Tai chimpanzees, who chose monkeys (red colobus and black-and-white colobus) almost exclusively.

Methods of hunting red colobus monkeys also differ across sites and have been extensively studied in Tai, Mahale, and Gombe. In general, chimpanzees mainly feed upon immature individuals or females when hunting red colobus monkeys (Uehara et al., 1992; Stanford, 1995). Chimpanzees at Mahale and Gombe seem to be more opportunistic and individualistic in their hunting, and commonly kill red colobus by flailing, smashing, or dragging the prey. In contrast, Tai chimpanzees join to search out monkeys and generally begin eating a colobus monkey while it is still alive (Uehara et al., 1992; Strier, 2003). Chimpanzees at Tai also intentionally search for more adult prey and hunt in larger groups with seemingly more cooperation. This could be an artifact of habitat differences, as red colobus monkeys are more easily cornered in the less dense canopies of Mahale and Gombe (Boesch and Boesch, 1989). In all areas, hunting occurs throughout the year, but is more frequent during the dry season months when other resources are more scarce (Stanford et al., 1994).

Predators greatly influence community composition by affecting the population dynamics of their prey species. For example, Teelen (2008) found that chimpanzee hunting at Ngogo, Kibale National Park greatly contributed to the decline in the population size of red colobus monkeys. As the numbers of monkeys continue to decline it is expected that the frequency with which chimpanzees hunt will be modified in order to sustain red colobus populations. Such shifting dynamics of prey populations can influence the availability of space and resources for other fauna. Therefore, the dynamics of chimpanzee interactions as both predators and prey are crucial for an understanding of their community ecology.

Competition. Most of the literature on competitive interactions involving chimpanzees centers on intraspecific competition between males and females. Documented interspecific competition between chimpanzees and other fauna is usually food related. Therefore, research in this area focuses on the relationships with other frugivorous animals, such as other primate species, birds, and smaller fruit-eating animals like squirrels and civets. Unfortunately, most chimpanzee research for interspecific competition is biased toward the relationships between sympatric chimpanzees and gorillas due to their supposed similar ecological niches as large-bodied apes, or toward relationships with other primates (i.e., overlooking non-primate fauna).

According to the competitive exclusion principle, previously discussed above, no two species can successfully occupy the same niche. Thus, the sympatry of chimpanzees and gorillas is an interesting occurrence that has been proposed to possibly contradict this principle. There is extensive overlap between gorillas and chimpanzees in diet, foraging height and even ranging (Table 4.2 in Morgan and Sanz, 2006 provides an extensive review of dietary overlap between chimpanzee and gorillas). Therefore, a high degree of competition between these two species would be expected and has even been proposed to be the cause of the relatively low densities of chimpanzees and gorillas in Lope, Gabon and Kahuzi-Biega, Democratic Republic of Congo (Kuroda et al., 1996; Cowlishaw and Dunbar, 2000). In actuality, little competition is observed. For example, chimpanzees and gorillas in Kahuzi use the same fruiting trees and occasionally meet each other at these trees, but no agonistic contacts have been observed (Yamagiwa et al., 1996). The lack of competition can be explained by slight differences in diet, foraging strategies, and ranging patterns as discussed below.

NICHE PARTITIONING IN CHIMPANZEE COMMUNITIES

As noted above, most information on niche partitioning in chimpanzee communities is limited to that between chimpanzees and gorillas. Information about spatial usage, habitat usage, dietary preferences, activity patterns, and other niche characteristics are available for specific taxa, but very few studies compare these qualities across taxa within a community, especially for chimpanzee communities.

One of the main differences between sympatric chimpanzees and gorillas is their ranging patterns. Gorillas forage, travel, and rest in a variety of habitat types, while chimpanzees are more restrictive in their preferences. For example, gorillas often enter swampy areas to feed, while chimpanzees avoid them (Yamagiwa et al., 1996). Additionally, gorilla groups tend to use small parts of their home range each month, covering the entire home range only over the course of a year while chimpanzees forage widely for fruit on a daily basis, covering large portions of their home range in a shorter time period (Stanford and Nkurunungi, 2003).

While their diets are generally similar, the specific compositions of food items eaten differ between chimpanzees and gorillas. In general, gorillas eat many leaf and bark species that are not consumed by chimpanzees, and chimpanzees eat many fruit and seed species not consumed by gorillas. Chimpanzees also feed on more kinds of insects (honey bees, ants, beetles, etc.) and prey upon mammals, which gorillas have not yet been seen to eat. Gorillas at Kahuzi-Biega were also observed feeding on several kinds of roots (trees, shrubs, and herbs) and rotten wood, which chimpanzees never ate (Kuroda et al., 1996; Yamagiwa et al., 1996; Yamagiwa and Basabose, 2006). This difference in diet is intensified during the dry season, with gorillas relying more heavily on foliage and bark than chimpanzees, that continue to consume mostly fruit (Tutin et al., 1991).

Only by examining communities through niche partitioning and interspecific interactions can we begin to understand particular behaviors and resource sharing and the application of such information beyond topics such as diet, activity patterns, habitat use, etc.

DRY-HABITAT OR “SAVANNA” CHIMPANZEES

Characteristics of dry-habitat chimpanzee communities. The term “savanna” refers to an ecosystem characterized by continuous undergrowth of grass, a discontinuous layer of trees and shrubs of variable height and density, and growth patterns that are closely associated with alternating wet and dry seasons (Mistry, 2000). In regards to chimpanzees, this term generally applies to sites with mean annual rainfall of less than1500mm and lengthy (i.e., $\geq$ 6 months) dry seasons (Moore, 1992; Pruetz, 2006). Additionally, these “savanna” sites are mostly mosaic environments, consisting of a mixture of grassland, gallery forests, and more closed woodlands. While the specific environmental composition may vary, all “savanna” chimpanzees are significantly more affected by water scarcity, extreme temperatures, and the presence of little to no canopy cover than forest-dwelling chimpanzees (McGrew et al., 1981). Due to the ambiguous nature of the term “savanna” within popular and scientific literature, I have chosen instead to use the term “dry-habitat” to describe such dry, open chimpanzee sites.

Kortlandt (1983) identified four areas within the chimpanzee distribution that have arid conditions and could contain savanna sites. These are: 1) a zone in southeastern Senegal and southwestern Mali, 2) an isolated site in the northwestern Central African Republic, 3) a zone to the east of the Central African Republic and southwest of the Sudan, and 4) an area west of the Ugalla-Mtambo River in Tanzania (Figure 2-4). Theses areas correspond with chimpanzee studies that are no longer ongoing (Filabanga, Tanzania: Suzuki, 1969; Kano, 1971, 1972 and Assirik, Senegal: McGrew et al., 1981; Baldwin et al., 1982; Tutin et al., 1983) and current ongoing research at Bafing, Mali (Duvall, 2000, 2001), Fongoli, Senegal (Pruetz, 2002; Pruetz et al., 2002; Piel, 2004), Ugalla, Tanzania (Moore, 1992; Hernandez-Aguilar, 2006; Stewart, 2011), and Semliki, Uganda (Hunt and McGrew, 2002).

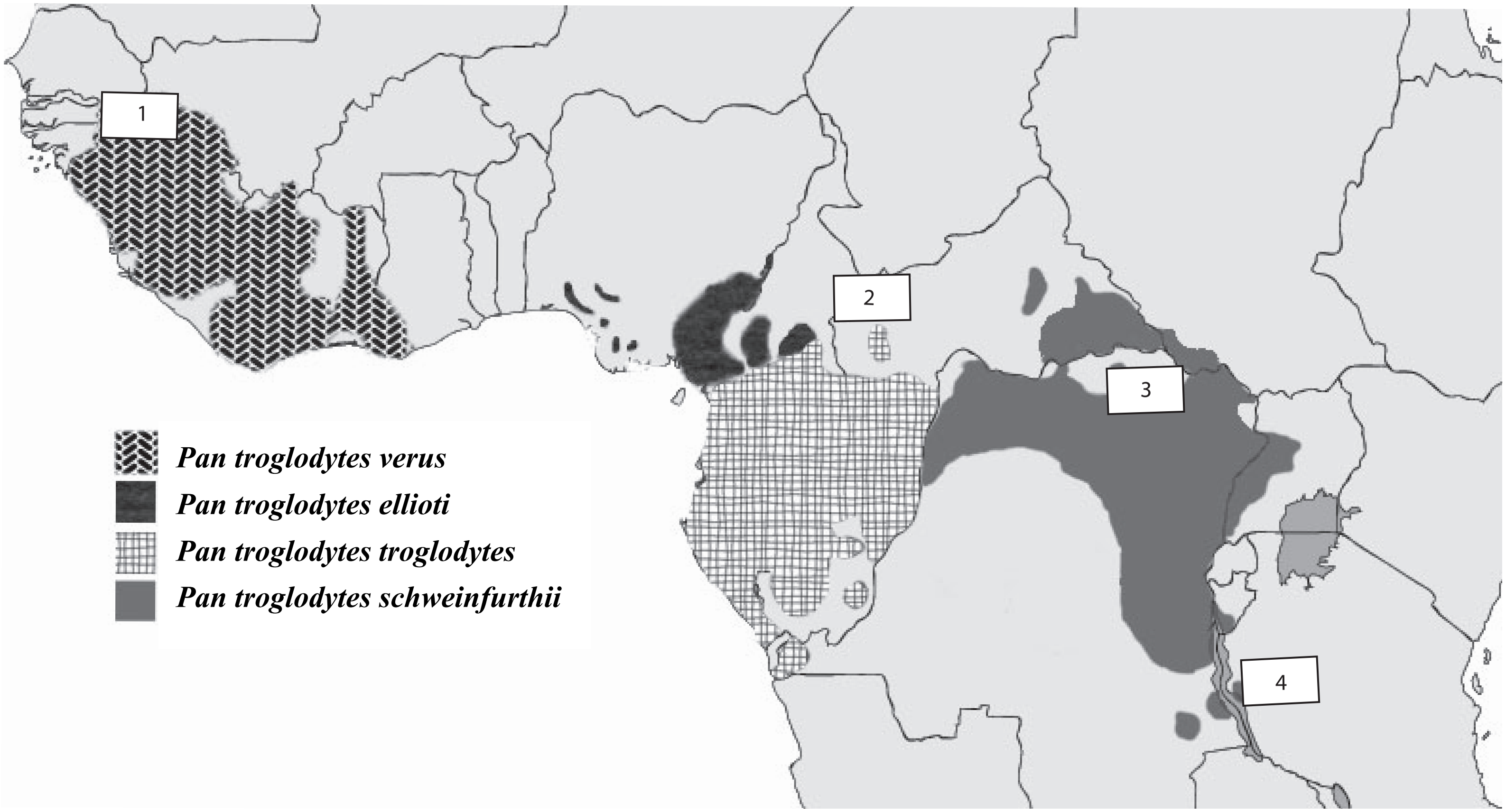


Figure 2-4. Map showing the approximation of the four areas within the distribution of chimpanzees that could contain dry-habitat sites, as determined by Kortlandt (1983). 1) zone in southeastern Senegal and southwestern Mali, 2) isolated site in northwestern Central African Republic (CAR), 3) zone to the east of CAR and southwest of Sudan, 4) area west of the Ugalla-Mtambo River in Tanzania.

Compared with chimpanzee populations living in more closed and/or wetter habitats, dry-habitat chimpanzees studied thus far have been found to generally consume fewer plant taxa, eat less meat, and have a more narrow diet in terms of total species, parts, and number of fruits eaten. Low levels of meat eating (possibly due to a lack of preferred vertebrate prey like red colobus monkeys) might be compensated by large amounts of invertebrate feeding, although the percentage of invertebrates in chimpanzee diets varies across sites (Moore, 1992; Pruetz, 2006). Dry-habitat chimpanzees also seem to have larger home ranges than other chimpanzees and slightly smaller party sizes (Baldwin, 1979).

Research importance. Research of dry-habitat chimpanzee communities has various implications for expanding the ecological knowledge of chimpanzees, aiding in conservation efforts, and yielding important insights into adaptations of early hominids.

Studies of chimpanzee diet, habitat use, and ranging behavior in marginal habitats will help determine how water availability, food availability and distribution, vegetative cover, and climate limit chimpanzee distribution. In addition, comparing different chimpanzee habitats can elucidate sources of variability in chimpanzee behavior (Moore, 1992; Hunt and McGrew, 2002). Furthermore, detailed examination of ecological variables can help determine the minimum requirements needed by chimpanzees to survive, and provide information on the ability of chimpanzees to adapt to differing environments (Hunt and McGrew, 2002).

Chimpanzees are often used as referential models for early hominins, as the last common ancestor (LCA) is thought to have been roughly similar to modern chimpanzees in overall body size, brain size, and diet (Kortlandt, 1983; Susman, 1987; Moore, 1992, 1996; Zihlman, 1996)). Additionally, the fact that some chimpanzees live in closed savanna-woodlands fits well with research showing that early hominins (e.g., *Australopithecus*, *Ardipithecus*) lived in closed woodland environments rather than open savannas (Stanley, 1992; Reed, 1997; Wynn, 2000; Aronson et al., 2008; Le Fur et al., 2009; White et al., 2009). Therefore, any behavioral differentiation of traits found in dry-habitat chimpanzees (as compared to other chimpanzees) due to "savanna characteristics" can give insight into scenarios of early hominin behavioral ecology (Moore, 1992, 1996).

RESEARCH QUESTION AND PREDICTIONS

This dissertation research specifically investigates the following question: What niche, or ecological role, do chimpanzees living in an open, dry savanna woodland environment occupy? To answer this question, associations between an arid, open environment and the main components of the chimpanzee niche (patterns of resource use and interspecific interactions) were examined. In order to better elucidate these relationships between environment and behavior, data collected at the savanna site of Issa, in western Tanzania (described in Chapter 3) are compared with published data from other chimpanzee populations (see Chapter 8).

HYPOTHESES AND PREDICTIONS

The general expectation that dry-habitat chimpanzees will have a broad realized niche can be broken down into two specific hypotheses and resultant predictions. For all hypotheses and predictions, statements are in comparison to chimpanzees from closed, wetter, forested sites.

Hypothesis A. Dry-habitat chimpanzees will use proportionally more spatial and dietary resources that are available to them.

Primates that live in habitats with resources that are patchily distributed in either space (i.e., throughout the habitat) or time (i.e., across wet and dry seasons) have been shown to change the composition of their diets by feeding on lower-quality or less preferred food items and alter foraging behavior by ranging further (Oates, 1987; Janson and Chapman, 1999; Strier, 2003). A savanna-woodland habitat presents chimpanzees with various resource patches that are of differing sizes and unevenly distributed throughout both space and time (McGrew et al, 1981). Therefore, the following predictions about dry-habitat chimpanzees can be made:

<u>Prediction A1</u>: Issa chimpanzees will use a relatively greater number of available food items, in terms of both floral and faunal species, and the parts of those species.

<u>Prediction A2</u>: The diet of Issa chimpanzees will consist of a relatively greater number of plant species that are considered to be scarce within their environment.

<u>Prediction A3</u>: Issa chimpanzees will use a relatively greater number of available habitat types for both food-related (i.e., foraging and feeding) and non-food-related (i.e., travelling, resting, nesting) activities.

Hypothesis B. Dry-habitat chimpanzees will have relatively more instances of negative interspecific interactions.

Since resources are more patchily distributed in a savanna-woodland habitat (McGrew et al., 1981), access to resources by chimpanzees will be greatly limited by the number of competitors that are trying to use those same resources. This should result in more instances of competition, but whether that is expressed as exploitative or interference competition has not been well studied. Instances of predation by chimpanzees (i.e., carnivory and/or insectivory) are expected to increase to compensate for scarcity and patchy distribution of vegetative dietary resources. Predation upon chimpanzees is also expected to increase due the presence of four large carnivores (i.e., leopard, lion, hyena, wild dog) in an open environment that provides greater visibility for predators and less cover for prey (Moore, 1996). Therefore, the following predictions about savanna chimpanzees can be made:

> Prediction B1: There will be more direct (interference) competition between Issa chimpanzees and sympatric species for both spatial and dietary resources.
>
> Prediction B2: There will be more indirect (exploitative) competition between Issa chimpanzees and sympatric species for both spatial and dietary resources.
>
> Prediction B3: There will be more predation by Issa chimpanzees on other fauna (including insects).
>
> Prediction B4: There will be more predation upon Issa chimpanzees by large carnivores.

In order to test predictions about resource use, data were first collected on the availability of resources at Issa by monitoring the distribution of potential habitat and food resources, and how this distribution changed throughout the year. Similarly, data on faunal species presence/absence at Issa were collected in order to test predictions about potential interspecific interactions. These data help determine the fundamental (i.e., potential) niche of Issa chimpanzees. Behavioral data on the actual resource use and interspecific interactions of Issa chimpanzees inform on their realized (i.e., actual) niche. Collection of all ecological and behavioral data is described in more detail in Chapter 4.

CHAPTER SUMMARY

Community ecology studies seek to explain the relationships between assemblages of species, or communities, and their environments. Patterns of resource use, niche differentiation, and interspecific interactions provide insight into how communities function and adapt to changing variables. Much information is known about chimpanzee social structure, demography, life history variables, cultural behaviors, foraging strategies, and diet, but little has been studied on habitat use (beyond nesting) and interspecific interactions (beyond prey/predator relationships). Furthermore, most of this chimpanzee research has focused on wet, forested sites as opposed to dry, open sites.

My research fills an important gap in the knowledge about resource use and interactions of chimpanzees, particularly those living in a highly seasonal dry-habitat at the site of Issa in western Tanzania. Determining the realized niche of Issa chimpanzees, and comparing that to the realized niche of other chimpanzee populations gives a better understanding of the chimpanzee fundamental niche, or the full range of their potential environments and adaptability.

CHAPTER 3: STUDY SITE

GEOGRAPHY

The research site of Issa (05° 23.34 S, 30° 35.04 E) was established by Hernandez-Aguilar in 2001 (Hernandez-Aguilar, 2006), and there has been a continuous research presence at the site since 2008 (Stewart, 2011). The main study area is approximately 85km^2, though my research focused on a slightly smaller part of this area of about 60km^2. Issa lies in the west of the Ugalla region in western Tanzania, east of Lake Tanganyika (Figure 3-1). While most of the Ugalla region falls within the Tongwe East Forest Reserve, the study site is on "general land" with no official status or protection (Kano, 1972; Stewart, 2011).

Ugalla is thought to be the easternmost distribution of chimpanzees in Africa, consisting of broad valleys in between steep mountains and flat hilltop plateaus (Massawe, 1992; Stewart, 2011). Most streams within the region are seasonal, with two permanent rivers (the Malagarasi River to the north and the Ugalla River to the west) forming the boundaries of the region (Kano, 1972; Massawe, 1992; Moore, 1994; Hernandez-Aguilar, 2006; Stewart, 2011).

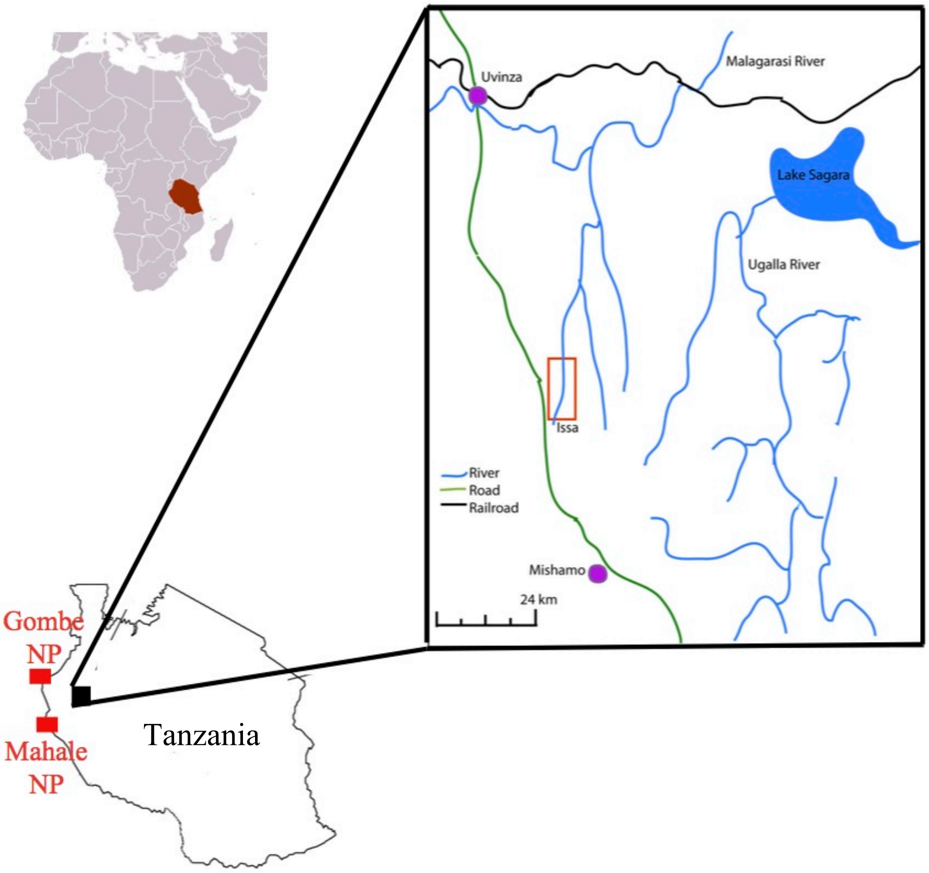


Figure 3-1. Location of study area, indicated by the open red rectangle, within the Ugalla region of Tanzania (after Hernandez-Aguilar, 2009). Note: not all rivers and streams are shown in this figure; NP: national park.

VEGETATION

Ugalla is generally characterized by “miombo” woodland vegetation (i.e., dominated by tree species of *Brachystegia*, *Julbernardia*, and *Isoberlinia)* with open canopy and grassy understory. The mosaic vegetation structure of the Issa study area consists of swamp, dry grassland, wooded grassland, miombo woodland, gallery forest, thicket forest, and hill forest, as described by Hernandez-Aguilar (2006, 2009). These last three vegetation types of “forest” comprise only 1.5% of the region, while the other “open” vegetation types comprise 98.5% of the study area as determined by GIS and ground-truthing by Pintea and Hernandez-Aguilar in 2007 (Hernandez-Aguilar, 2006, 2009; Ogawa et al., 2007). For this study, only the categories of grassland/swamp, woodland, and forest were used (Table 3-1) to simplify distinctions between “open” and “closed” habitat types. Therefore, the distribution of habitat types used for my study is: 90.5% woodland, 1.5% forest, and 8% grassland/swamp. Woodland and forest vegetation occur in each topographic level (i.e., valley, slope, plateau), while grassland/swamp vegetation is found only in broad open valleys (Figure 3-2).

Table 3-1

Vegetation types in Issa (from Hernandez-Aguilar, 2006, 2009; Stewart, 2011)

Issa vegetation types	This study
Hill forest: evergreen and semi-deciduous species growing on the edges of escarpments	**Forest**
Thicket forest: evergreen and semi-deciduous vegetation, dominated by lianas and climbers	
Gallery forest: evergreen forest with open understory, usually along seasonal water courses	
Woodland: deciduous trees and shrubs with grass understory and discontinuous canopy	**Woodland**
Wooded grassland: dominated by grasses with isolated shrubs and trees	**Grassland/ Swamp**
Dry grassland: short grasses with isolated shrubs in broad valley lowlands or high plateaus	
Swamp: tall grasses up to 3m. Permanently inundated, with few scattered trees or shrubs.	

Figure 3-2. Issa vegetation. Left: miombo woodland surrounding a thin strip of forest originating in the valley and stretching up the mountain slope; Right: swamp (indicated by white rectangle) in the valley, miombo woodland slope in foreground.

CLIMATE

Ugalla is one of the driest, most open, and seasonal habitats inhabited by chimpanzees, representing a unique and relatively extreme set of environmental conditions for chimpanzees (Kano, 1972; Itani, 1979; McGrew et al., 1981; Nishida, 1989; Moore, 1992, 1994, 1996; Hernandez-Aguilar, 2006, 2009; Ogawa et al., 2007; Stewart, 2011). Average daily temperatures at Ugalla range from 11–35°C (Rudicell et al., 2011; Stewart, 2011). In 2006, Hernandez-Aguilar reported mean daily maximum temperature was highest in August (34°C) and lowest in November (28°C). Mean daily minimum temperature was highest in January (17.2°C) and lowest in August (14.4°C) (Hernandez-Aguilar, 2006, 2009; Ogawa et al., 2007). In 2011, Stewart reported mean daily maximum temperature was highest in October (29°C) and lowest from February to April (24°C). Mean daily minimum temperature was also highest in October (18°C), but lowest in July (14°C). Average daily minimum and maximum temperatures were found to be lower in forested areas as compared to woodland areas, with plateaus and valleys having the coldest temperatures (Stewart, 2011).

Annual rainfall in the area is typically less than 1000mm; Hernandez-Aguilar (2006, 2009) reported 955mm average annual rainfall and Ogawa et al. (2007) reported an average annual rainfall of 980mm for the whole Ugalla region from 1973-2005. The rainy season lasts from October to April and the dry season (months with less than 100mm of rainfall) lasts for five months, from May to September (Hernandez-Aguilar, 2006, 2009; Ogawa et al., 2007; Stewart, 2011; Stewart et al., 2011). During the dry season almost all but the largest streams within the study area completely dry up, making the location of available water sources extremely influential on the foraging and ranging behaviors of local fauna, including chimpanzees.

NON-CHIMPANZEE FAUNA

In more recent years, the Ugalla region has been greatly affected by human disturbance, including agricultural expansion, fire, cattle herding, logging, and poaching. Using snares is the most common practice for poaching, but large game such as buffalo (*Syncerus caffer*) and bushbuck (*Tragelaphus scriptus*) are also hunted with firearms (personal observation, this study; Hernandez-Aguilar et al., 2006; Stewart, 2011). As such, the numbers and kinds of animals present in the region have changed since researchers first established the study site. Table 3-2 includes large to medium sized mammal and frugivorous bird species that were seen during this current and previous studies. As noted in the table, some of the larger mammal species (e.g., elephant-*Loxodonta africanus*, zebra-*Equus burchelli*, topi-*Damaliscus lunatus*) were not seen during this study, and are perhaps now absent from the area. Additionally, among the potential chimpanzee predators (i.e., lion, leopard, hyena, and wild dog), no evidence of the presence of wild dog was seen during this study. Appendix A lists these fauna, in addition to other fauna present at Issa that were not used for analyses in this study (e.g., small mammals, non-frugivorous birds, reptiles, etc.).

Table 3-2

Large and medium sized mammals and frugivorous birds recorded in Ugalla during current and previous studies (modified from Hernandez-Aguilar, 2009; Stewart, 2011). Evidence: N-not seen in current study; DO-direct observation; I-indirect evidence (e.g., feces, prints, feathers, quills, burrows, vocalizations); C-camera trap photo/video. Taxonomy based on Groves, 2001; Groves and Grubb, 2011

Class **Order** *Species*	Common name	Evidence
Mammalia		
Artiodactyla		
Alcelaphus lichtensteinii	Lichtenstein hartebeest	DO, I, C
Philantomba monticola	Blue duiker	DO, I, C
Damaliscus lunatus	Topi	N
Hippotragus equinus	Roan antelope	DO, I, C
Hippotragus niger	Sable antelope	N
Kobus ellipsiprymnus	Defassa waterbuck	DO, C
Oreotragus oreotragus	Klipspringer	DO, I, C
Ourebia ourebi	Oribi	N
Phacochoerus africanus	Warthog	DO
Potamochoerus larvatus	Bushpig	DO, I, C
Redunca redunca	Bohor reedbuck	DO, I
Madoqua kirki	Kirk's dikdik	N
Sylvicapra grimmia	Grey (bush) duiker	DO, I, C
Syncerus caffer	African buffalo	I, C
Taurotragus oryx	Eland	I
Tragelaphus scriptus	Bushbuck	DO, I, C
Carnivora		
Aonyx capensis	African clawless otter	I
Bdeogale crassicauda	Bushy-tailed mongoose	C
Canis mesomeles	East African black-backed jackal	DO, I
Civettictis civetta	African civet	I, C
Crocuta crocuta	Spotted hyena	I
Felis serval	Serval	C
Felis sylvestris	African wild cat	I
Genetta genetta	Common genet	I, C
Helogale parvula	Dwarf mongoose	DO, I, C
Herpestes ichneumon	Lesser mongoose	DO, I
Herpestes naso	Long-snouted mongoose	C
Herpestes sanguinea	Slender mongoose	C
Lycaon pictus	East African wild dog	N
Mellivoria capensis	East African honey badger	I
Panthera leo	Lion	I, C
Panthera pardus	Leopard	DO, I, C

Class **Order** *Species*	Common name	Evidence
Hyracoidea		
Dendrohyrax arboreus	Tree hyrax	DO, I, C
Heterohyrax brucei	Yellow spotted hyrax	I
Perissodactyla		
Equus quagga	Zebra	N
Pholidota		
Smutsia temminckii	Ground pangolin	I, C
Primates		
Chlorocebus aethiops	Vervet monkey	DO, I, C
Cercopithecus ascanius	Red-tail monkey	DO, I, C
Cercopithecus mitis	Blue monkey	DO, I
Galago senegalensis	Senegal galago	DO, I, C
Otolemur crassicaudatus	Greater galago	DO, I, C
Pan troglodytes schweinfurthii	Eastern chimpanzee	DO, I, C
Papio cynocephalus	Yellow baboon	DO, I, C
Procolobus tephrosceles	Red colobus	DO, I
Proboscidea		
Loxodonta africana	African bush elephant	N
Rodentia		
Heliosciurus sp.	Sun squirrel	DO
Hystrix africaeaustralis	Porcupine	I, C
Paraxerus cepapi	Smith's bush squirrel	DO
Protoxerus stangeri	Giant forest squirrel	DO
Tubulidentata		
Orycteropus afer	Ant-bear (aardvark)	I
Aves (Birds)		
Bucerotiformes		
Bucorvus leadbeateri	Southern ground hornbill	DO, I
Ceratogymna bucinator	Trumpeter hornbill	DO, I
Tockus nasutus	African grey hornbill	DO, I
Columbiformes		
Treron calvus	African green pigeon	DO, I
Turtur chalcospilos	Emerald-spotted wood dove	DO, I
Streptopelia capicola	Ring necked dove	DO
Musophagiformes		
Musophaga rossae	Ross's turaco	DO, I
Tauraco schalowi	Schalow's turaco	DO, I
Passeriformes		
Poicephalus meyeri	Brown parrot	DO, I
Pycnonotus pycnonotus	Common bulbul	DO, I

ISSA CHIMPANZEES

Although there has been a continuous research presence at Issa since 2008, the Issa population of chimpanzees remains unhabituated. Therefore, little information is known about its population structure. However, genetic analyses conducted on fecal samples collected throughout the study area in previous years were used to conservatively identify 67 individuals, including 31 females, 27 males, and 9 individuals whose sex could not be determined (Rudicell et al., 2011; Stewart, 2011).

All individuals are considered to be part of one continuous population with an estimated home range of between 278km^2 and 750km^2 (Kano, 1972; Itani, 1979; Baldwin et al., 1982; Hernandez-Aguilar, 2006, 2009; Ogawa et al., 2007; Rudicell et al., 2011; Stewart, 2011; Stewart et al., 2011). The large variation in estimated home range size is mainly due to the varied chimpanzee densities given by researchers, since home range size for unhabituated chimpanzees is determined by combining density and population size estimates. For example Kano (1972) estimated a density of 0.08 individuals/km^2, while Yoshikawa et al. (2008) and Ogawa et al. (2007) state a density of 0.09 individuals/km^2. In a study using nest counts to determine density, Stewart (2011) estimated a density of 0.14 individuals/km^2. Using a minimum density of 0.03 individuals/km^2 and maximum density of 0.14 individuals/km^2, along with the total area of the Ugalla region (about 3352km^2), the total population size of chimpanzees in the Ugalla region (and therefore, at Issa) is estimated to be between 100 and 470 individuals (Hernandez-Aguilar, 2006). It is presumed that the structure of this, and other, dry-habitat chimpanzee populations resembles that of forest chimpanzees, with members of a single population ranging in fluid sub-groups over a specific geographic area (Stewart, 2011).

Previous studies of Issa chimpanzees have focused on documenting characteristics of the study area (Hernandez-Aguilar, 2006) and describing the nesting patterns of Issa chimpanzees, particularly focusing on location and re-use of nests (Hernandez-Aguilar, 2006, 2009; Stewart, 2011). Hernandez-Aguilar (2006) has also presented some dietary information based on fecal samples of Issa chimpanzees; the results of her study, as compared to my study, are discussed in Chapter 5. While the presence of non-chimpanzee fauna was noted during previous studies, no research has yet addressed the roles these fauna might have in influencing chimpanzee behavior. My study, therefore, fills in the gaps of knowledge about Issa chimpanzee habitat use for non-nesting behavior, adds to the understanding of their diet, and provides important information about interspecific interactions between chimpanzees and other fauna.

CHAPTER 4: DATA COLLECTION AND ANALYSES

PATCH FOCALS

Most primatological studies employ methodologies that include actively following the species of interest. This practice is not sufficient for community ecology studies, however, as it overlooks certain phenomena, such as indirect competition, that occur in areas important to the focal species when they are not immediately present. Therefore, this study did not conduct focal follows of chimpanzees, but instead focused on important areas or resource patches for chimpanzees (described below).

While continuously following chimpanzees would allow researchers to determine what resources the chimpanzees are using, focusing on resource patches can capture not only resources that chimpanzees actively use (through direct observation), but also the other faunal species, if any, that use those same resources when the chimpanzees are not present. This allows for possible chimpanzee competitors to be better identified and can inform researchers about the choices chimpanzees make about which resources to use. For example, chimpanzees may actively avoid a resource patch if too many potential competitors visit that same patch, and instead may choose to visit a different patch. Furthermore, focusing on different patches provides the opportunity for observing animals that might be displaced from a patch upon the arrival of chimpanzees; researchers following behind a chimpanzee group could easily miss this occurrence. Additionally, systematically sampling resource patches throughout the study area ensures that resources that are *not* used by the chimpanzees, but are perhaps used by other species, are also studied; actively following chimpanzees allows for the identification of such unused resource areas, but does not capture how those areas are used by other species in the community.

Resource patch focal observations are also better suited for study sites with chimpanzees (and other species) that are unhabituated or only partially habituated to the presence of researchers. By focusing on resource patches, data collection is maximized; even observations of an "empty" patch (i.e., not visited by any animals) results in meaningful data that indicate non-use of a particular resource patch or area within the habitat. Resource patches can also be observed from a distance (depending on visibility), which increases the probability that researchers will remain undetected by the study subjects.

To further evaluate the validity of using patch focals, I compared the encounter rate of both chimpanzees and other fauna using three different methods over a period of one year: "Listen & Follow", in which researchers go to a specific location to listen for chimpanzees, and then find and follow the group if possible; patch focals, as described below; and digital camera traps (Russak et al., 2012). Encounter rate was calculated by dividing the total number of animal encounters by the total observation hours for each method (Table 4-1). An encounter was defined as the observation of a new individual, or if an individual identification could not be made, an observation occurring after at least one minute of no animal presence.

Table 4-1
Total number of encounters and encounter rates for three different methods used to observe fauna at Issa

Method	**Total Hours**	**Non-Chimpanzee Encounters**	**Rate**	**Chimpanzee Encounters**	**Rate**
Camera Traps	107926	1934	0.015	250	0.003
Patch Focals	2175	99	0.049	12	0.004
Listen & Follow	496	114	0.228	55	0.104

"Listen & Follow" had the highest encounter rates for both chimpanzee and non-chimpanzee fauna, while camera traps had the lowest encounter rates. While patch focals had intermediate encounter rates for chimpanzees, rates from patch focals did not differ significantly from chimpanzee encounter rates for camera traps; all other comparisons between the three methods were significantly different ($p<0.01$, Kruskal-Wallis and Tukey's HSD). These differences in encounter rates are likely due to biases in how these methods are employed. For example, "Listen & Follow" is used in areas where chimpanzees are assumed to be located, based on previous sightings and vocalizations. In contrast, patches are randomly distributed throughout the study site, located in areas that may or may not be near trails or in locations known to be frequented by chimpanzees. Camera traps are also located throughout the study site, but purposefully placed near animal trails, so it is surprising that this method had the lowest encounter rates.

It is important to note that in addition to encounter rates, the quality of data also differs between these three methods. For example, researchers may encounter more fauna with the "Listen & Follow" method, but these animals are usually running away from the observer. By remaining in one location during patch focals, researchers have the opportunity to observe animals behaving as they normally would without the presence of researchers scaring them. Therefore, a method such as “Listen & Follow” is informative for a species-specific study in which animals are habituated, particularly at sites where researchers know where animals are located, and are thus able to direct search efforts. Community ecology studies, like my research, are better informed by a method such as patch focals, which results in data for the entire community as opposed to one or a few species. Additionally, patch focals are particularly useful for research at sites (e.g., Issa) with unhabituated animals that will not tolerate being constantly followed by researchers.

PATCH CHARACTERISTICS

After superimposing a grid on a map of the study site, a total of 100 potential patches were randomly plotted; from these 100 points, 50 were randomly chosen as patches to be observed during the study period, stratified for habitat type and chimpanzee use so that both heavily utilized and non-utilized patches were represented (Figure 4-1). Of these 50 patches, 37 were 50m x 50m with one patch located in forest and the rest in woodland habitat. Due to visibility constraints, the remaining 13 patches were 30m x 30m, with 11 patches located in forest and the rest in woodland habitat. Thus, the 38 woodland patches and 12 forest patches sampled covered a total area of 104,200m^2 (or 0.1042km^2), representing 0.2% of the total area within the site. Each patch was visited for three consecutive days to capture any repeated usage of an area, and sampled for a total of six days each (three days in the dry season and three days in the wet season).

Observations were from a distance that made the entire patch clearly visible, which varied according to the terrain, ranging from 30 to 60 meters from the patch edge.

The GPS coordinates of the plotted patches from Figure 4-1 are based on the center tree of each patch, which was also given a numbered aluminum tree tag for future reference. From this center tree, using a metric measuring tape, the southwest, southeast, northwest, and northeast corners, as well as the midpoints between these corners (i.e., directly north, south, east, and west of the center) were marked with biodegradable flagging tape. This ensured that the patch boundaries could be easily seen from the observation point. Within each patch the number, species (if known), and exact location of resources (e.g., trees, shrubs, termite mounds, water sources) in relation to the center tree were recorded. Measurements of DBH (diameter at breast height, about 1.5m) were taken for each individual tree or shrub ≥5cm DBH using a Lufkin metric diameter tape. For these same trees and shrubs, height was measured from the base of the tree/shrub to the highest leaf using an Invicta Plastics clinometer and the corresponding trigonomic equation [tree height = (distance from tree base to observer * tan (degree reading from clinometer)) + height of observer].

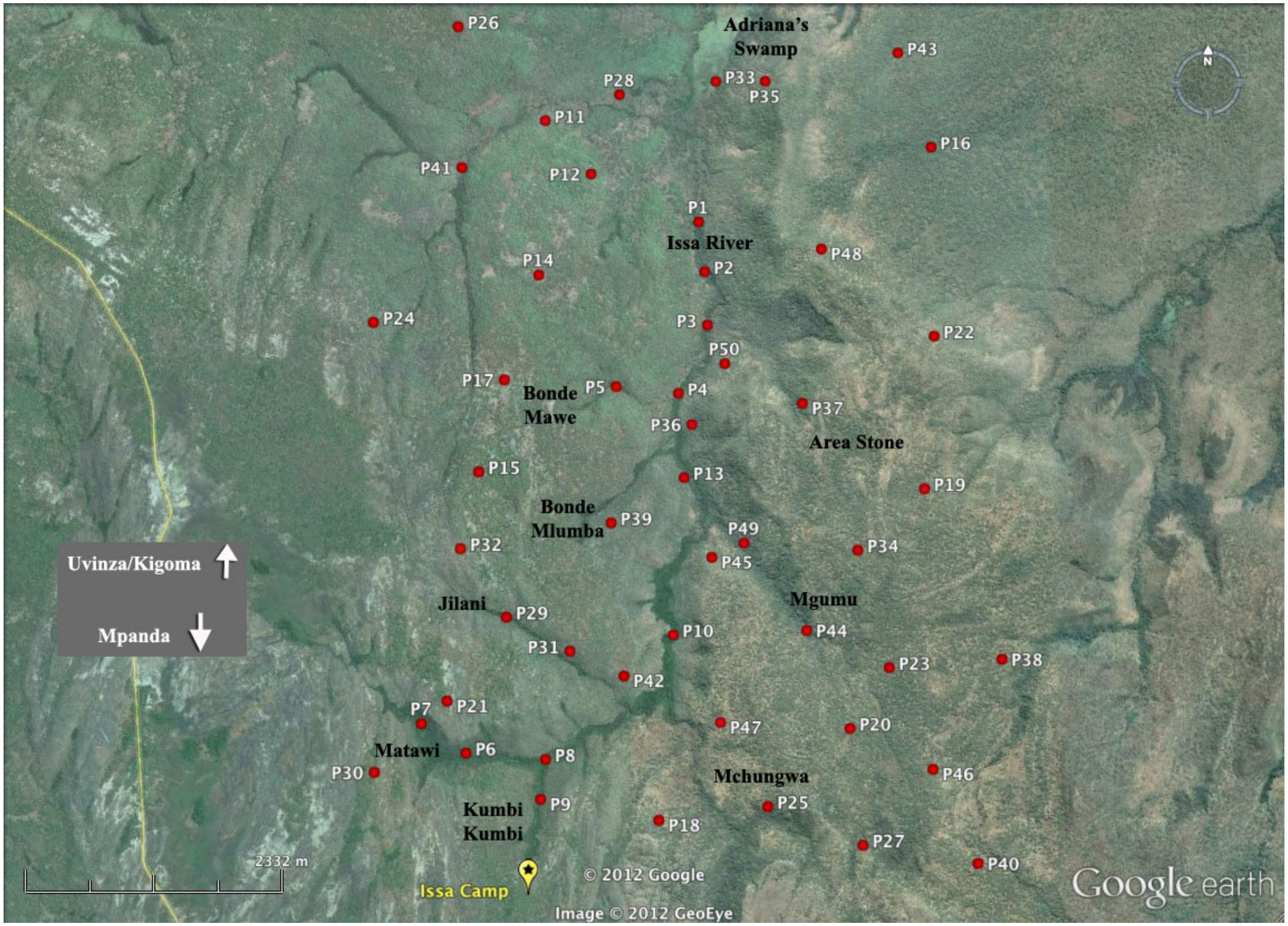


Figure 4-1. Locations of 50 patches; yellow line indicates the major road in the area; research camp is indicated in yellow.

BEHAVIORAL OBSERVATIONS

All data were collected during daylight hours due to difficulty with visibility at night and increased risk of attack by large nocturnal predators. To account for the potential instances of indirect competition or other interspecific interactions occurring at night, indirect data were also collected (described below). I and/or one of two field assistants collected all data; inter-observer reliability was evaluated monthly using the kappa coefficient (Kraemer, 1979; Martin and Bateson, 1993). For all months, $\kappa \geq 0.8$; therefore no data were omitted.

On observation days, patches were continuously monitored from early morning to early evening; start time and end time were recorded and used to calculate total observation time for that day. When an animal entered the patch, behavioral data were recorded using instantaneous scan sampling at one-minute intervals (Altmann, 1974). These data included the number and species of animals present, limited in this project to medium-to-large sized mammals and birds that are potential competitors and/or prey of chimpanzees (small mammals and birds are too difficult to accurately observe from a distance and are likely not main competitors of chimpanzees; see Table 3-2 in Chapter 3). The location of each individual in relation to the center tree (i.e., distance and direction), and its vertical location within the patch (i.e., ground, tree trunk, lower branches, middle of tree, or upper canopy) were also noted. The activity of each individual was recorded as travel, rest, eat, or other. For "eat", the type of plant matter being eaten (i.e., tree, shrub, herb, liana, and climber or vine; McGrew et al., 1988; Hernandez-Aguilar, 2006), plant species (if known), and plant part (i.e., fruit, flower, seed/pod, leaf/shoot, stem/stalk, and bark/cambium; McGrew et al., 1988; Hernandez-Aguilar, 2006) were recorded. Rare behaviors including threats, fights, and play, were also documented as they occurred; all behaviors are defined in Table 4-2.

Table 4-2
Ethogram of behaviors recorded during this study

Behavior	**Definition**
Travel	Movement from one location to another, can be walking or running
Rest	Little or no gross movement, posture variable
Eat	Placement of food item in mouth
Threat	Aggressive interaction with no contact (e.g., open mouth showing teeth, shaking branches, lunging)
Fight	Aggressive, vigorous contact with hands, feet, and/or mouth
Play	Low intensity slapping, wrestling, and/or lunging in the absence of aggression. Usually accompanied by "play face" (open mouth, relaxed lips) and/or laughing
Allogroom	One animal manipulates fur, extremity, or orifice of another
Other	Any behavior not listed above

To augment data on the presence of animal species within the study area, encounters with animals on the way to or from a patch were documented; for each encounter a GPS point was taken and the number and species of animals present were recorded. During patch observations, data on vocalizations of animals occurring outside of the patch were also recorded including the distance and direction from the patch center.

INDIRECT DATA COLLECTION

SCAT, PRINTS, AND OTHER SIGNS

Indirect data of species presence, as well as dietary diversity, were collected via fecal samples, feeding remains, prints, and other signs (e.g., feathers, quills, etc.) during examination of the focal patch before and after the sampling period (and as they were encountered). Identification of items was aided by the use of field guides (e.g., Kingdon 1997; Stuart and Stuart, 2000).

Fecal samples and feeding remains were collected as defined by McGrew et al. (1988, 2009). Using rubber gloves, feces were collected in plastic bags, and then tagged with the collection date, identification number, and GPS location. Feces were then washed in $1mm^2$ mesh sieves at the stream by camp or in a water bucket within one day of collection, before samples became dry. Food items present were photographed and then identified either through comparison with fresh plant material or published photographs/descriptions, or described in detail for later identification. The wet weight, estimated percent fecal matter volume, and estimated percent fiber volume (from terrestrial herbaceous vegetation, THV) were recorded for each sample. Additionally, the presence of invertebrates, fruit skins, and chewed leaves were rated as “none, few, some, or many”; these descriptive categories roughly correspond to 0%, 1-29%, 30-69%, and 70-100% of the sample. This qualitative assessment was also used for the presence of seeds from *Ficus* sp., as these seeds are extremely small and nearly impossible to count individually. All other seeds were counted individually and identified to species level, if possible, or given a seed number to be later identified (Stewart, 2011).

CAMERA TRAPS

Indirect data of species presence were also collected via remote digital camera traps that were placed at various sites throughout the duration of the study (Figure 4-2). Between 15 and 24 Bushnell Trophy Cams (model XLT GAME CAMERA 119456C) were deployed each month, capturing both diurnal and nocturnal animal encounters (Figure 4-3). All cameras were set to “normal” sensitivity level, and most were set to record 60-second video clips; a few cameras were set to take still photographs at one second intervals. Upon deployment, the height of the camera (between 0.9m and 1m), the direction it faced, and GPS location were recorded. Some examples of camera trap photographs are presented in Appendix C.

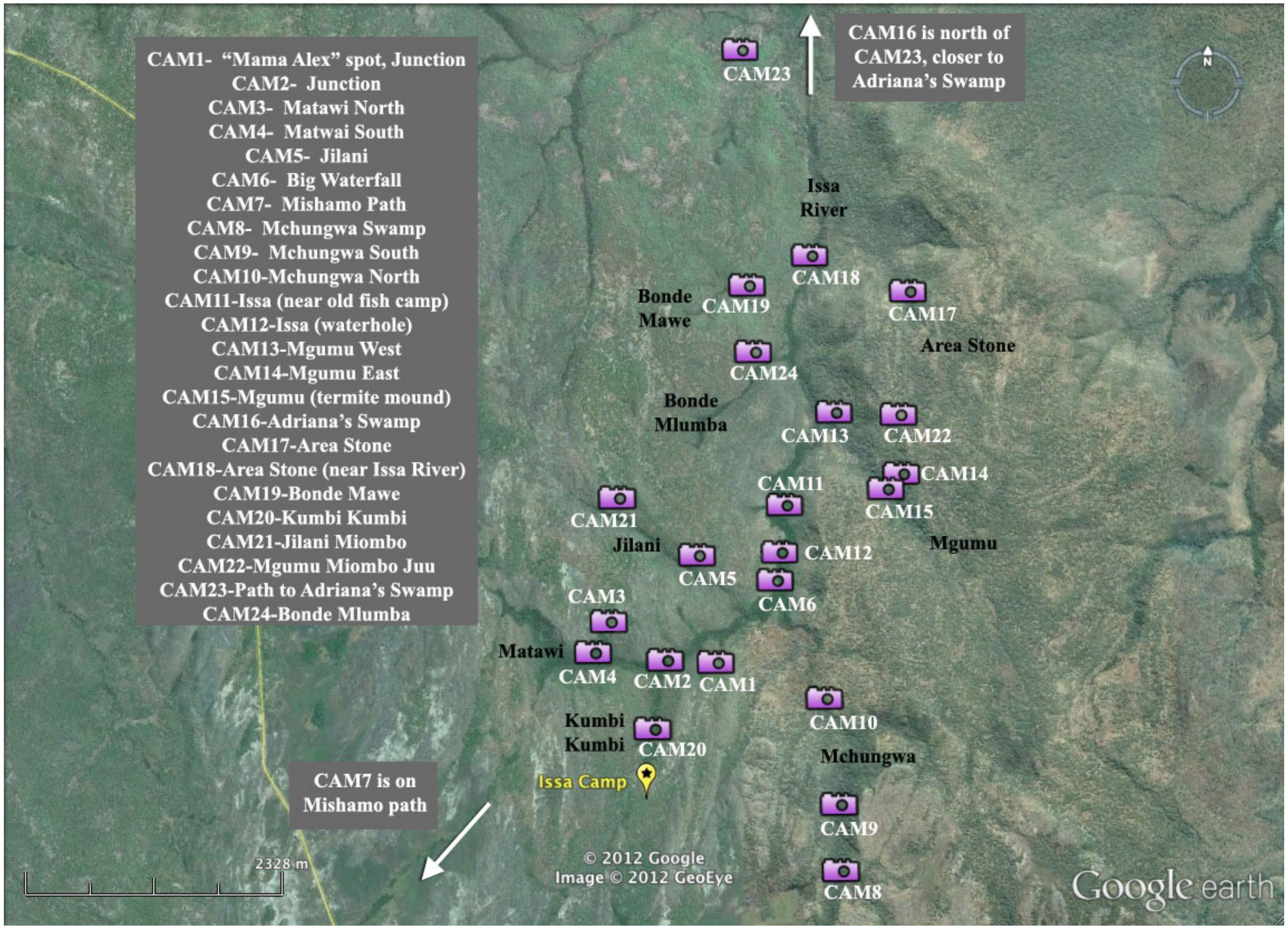


Figure 4-2. Locations of digital camera traps throughout the study site; not all cameras were deployed at the same time.

Figure 4-3. Setup of digital camera trap (camera is encased in plastic container for weather protection).

CLIMATE AND PHENOLOGY

CLIMATE

Daily rainfall was recorded continuously using a Hobo data-logging rain gauge (RG-3) located in the center of our camp. Six Hobo temperature and relative humidity loggers (H8 Pro series) were deployed throughout the study area in locations representing two vegetation types (woodland and forest) and three topographic levels (plateau, slope, and valley) for each vegetation type. Each logger recorded data every 30 minutes.

PHENOLOGY

At the start of each three-day sampling period, the relative abundance of plant parts (mature leaves; young or new leaves; flowers; and fruits, pods or seeds) for each patch was scored on a scale of 0 to 5, with 5 being the maximum amount possible for every individual monitored (modified from Chapman et al., 1994, as in Hernandez-Aguilar, 2006). Phenology data also came from trees along three line transects previously established by Stewart (2011) that were monitored monthly.

COMPARATIVE DATASET

All data collected at Issa, Ugalla are compared with previously published data from the forested chimpanzee sites of Tai, Kibale, and Budongo; the mosaic chimpanzee sites of Gombe and Mahale; and the savanna-woodland site of Assirik, Semliki, and Fongoli. Only qualitative comparisons are made, due to difference in methods used for data collection across sites.

ANALYSES

ENCOUNTERS

Encounters of chimpanzees and other fauna occurred both directly (i.e., direct visual observations and camera trap photos/videos) and indirectly (i.e., vocalizations and the presence of prints, feces, feeding remains, and/or other signs). For all direct observations, an independent encounter was defined as the observation of one or more individuals of a particular species at a certain location, in which none of these individuals had been previously observed within the prior five minutes. For patch focals, independent encounters were obtained by combining sequential data points from the one-minute scans into artificial five-minute bouts, particularly to avoid temporal autocorrelation (after Hunt, 1992; McGraw, 1996; Cant et al., 2001). The number of individuals present for each bout/encounter was noted as the maximum number present over the combined scans, and behavior was noted as the most frequent behavior across all individuals present for each bout.

Camera trap photos/videos were considered to be independent encounters when occurring at least 30 minutes apart. Camera trap intervals are longer than those for direct visual observations based upon currently accepted methods. Cameras offer a more limited view of animals present than direct visual observations, so it is easier to mistake an animal that simply went out of sight for a second individual, particularly with species that are difficult to identify individually. Increasing the time interval allowed between independent events decreases the likelihood that this error will be made (Jauhiainen and Korhonen, 2005; Ridout and Linkie, 2009; O'Connell et al., 2011; Gerber et al., 2012; Mugerwa et al., 2013). For all indirect observations, data were considered to be independent encounters when occurring in a location not previously recorded on that same day.

RESOURCE USE

Patterns of habitat use were based on the number of encounters of each animal species within a habitat type, and when available, the percentage of total time spent in each habitat type. To determine habitat preferences, Chi-square analyses were performed using the statistical program R, comparing observed number of encounters in each habitat type to an expected number of encounters based on habitat availability. These analyses were done with encounters for the entire year of study, as well as for encounters during the dry or wet season only to examine season differences. Yates correction for continuity was used only when degrees of freedom were equal to 1 (e.g., in woodland vs. forest patch analyses); this correction was not appropriate when degrees of freedom were greater than 1 (e.g., in whole site analyses with three habitat types) (Krebs, 1999; Zar, 1999).

Use of dietary (food) resources was determined by using direct observations of feeding events by chimpanzees and other fauna, as well as through the analysis of fecal samples (discussed above). However, due to a limited number of direct feeding observations, determination of the proportion of dietary components for all fauna was restricted to fecal sample analyses.

INTERSPECIFIC INTERACTIONS

Instances of neutral, mutualistic, and predatory interactions are qualitatively described. To assess the occurrence of direct competition, the amount of time spent behaving in a competitive manner (e.g., threat, display, fight, etc.) while in the presence of potential competitors was used as a proxy for direct competition. The percent of spatial and dietary overlap between chimpanzees and other fauna was used to assess indirect competition.

Spatial overlap was determined using Czekanowki's index, which provides an assessment of the symmetrical overlap of resource use between two species (Krebs, 1999; Carmago, 1995). The formula is:

$$O_{12} = O_{21} = 1 - ½ \Sigma \left| p_{1j} - p_{2j} \right|$$

where O is the overlap of species 1 and 2, and p_{1j} is the proportion of all encounters of species 1 in patch j. Values of O range from 0 (no overlap) to 1 (complete overlap). Only data from patches were used in this analysis, due to the unsystematic nature of data collection when outside of patches.

Dietary overlap was determined using Pianka's index, which provides an assessment of the amount of overlap in the diet of two species (Pianka, 1973; Krebs, 1999; Tarnaud, 2004). The formula is:

$$O_{jk} = \Sigma\ p_{ij}p_{ik}/(\Sigma p_{ij}^{2} \Sigma p_{ik}^{2})^{1/2}$$

where O is the overlap of species j and k, and p_{ij} is the proportion of food item i in the diet of species j and k. Again, values of O vary between 0 (no overlap) and 1 (total overlap). Only data from fecal sample analyses were used.

CHAPTER 5: ISSA CLIMATE AND RESOURCES

Abiotic factors, such as rainfall and temperature, greatly affect the availability and distribution of spatial and dietary resources, which in turn largely determine patterns of resource use. Therefore, an understanding of how abiotic factors change over time is a necessary step towards establishing the niche of any species.

CLIMATE

RAINFALL AND SEASONALITY

Rainfall data were continuously recorded throughout the study period from November 2010-October 2011. However, due to a technical malfunction with the logger, data were lost from November 2010 to December 2010; therefore, in order to capture a full annual cycle of rainfall, data presented here are from January 2011 to January 2012 (Figure 5-1).

Overall annual rainfall in Issa during this period was 1537mm. This amount is similar to that found by Stewart (2011), but is much higher than previously reported annual rainfall for the area (955mm: Hernandez-Aguilar, 2006, 2009; 980mm: Ogawa et al., 2007). In addition to an increased amount of yearly rainfall as compared to previous years, there was also an increase in the length of the dry season (i.e., months with less than 100mm of rainfall) during the study period. In the past, the dry season has typically been five months, lasting from May to September (Hernandez-Aguilar, 2006, 2009; Ogawa et al., 2007; Stewart, 2011; Stewart et al., 2011); during this study period, from November 2010 to October 2011, the dry season lasted six months, from April to September (Figure 5-1). These data indicate that both the wet and dry seasons at Issa were more extreme during this study period than in previous years (i.e., the wet season was more rainy, and the dry season was more dry).

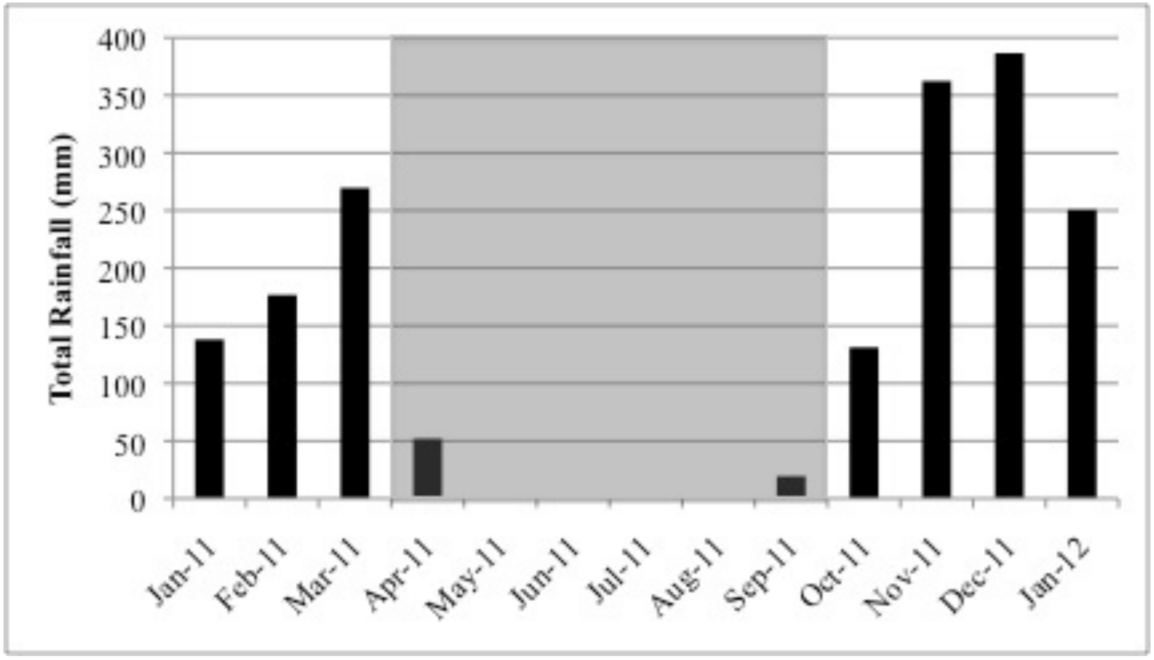


Figure 5-1. Monthly rainfall in Issa from January 2011 to January 2012. Dry season (i.e., months with less than 100mm rain) indicated by shaded grey box.

TEMPERATURE

During the study period from November 2010 to October 2011, an absolute range of 12-36°C was recorded in Issa. When averaged across data loggers, mean daily maximum temperature was highest at the end of the dry season and lowest at the end of the wet season (31°C in September and 23°C in March, respectively). Mean daily minimum temperature was also highest at the end of the dry season (18°C in September), but was lowest in the middle of the dry season (14°C in July). In almost all instances, daily temperatures in forest were lower than those in woodland (Figure 5-2).

In general, the temperature data during this study period were similar to that presented by Stewart (2011), but show a slight trend towards hotter temperatures occurring earlier in the year (i.e., higher mean daily maximum and minimum temperatures occurred in September rather than October). This pattern is perhaps correlated with the earlier onset, and increased length, of the dry season.

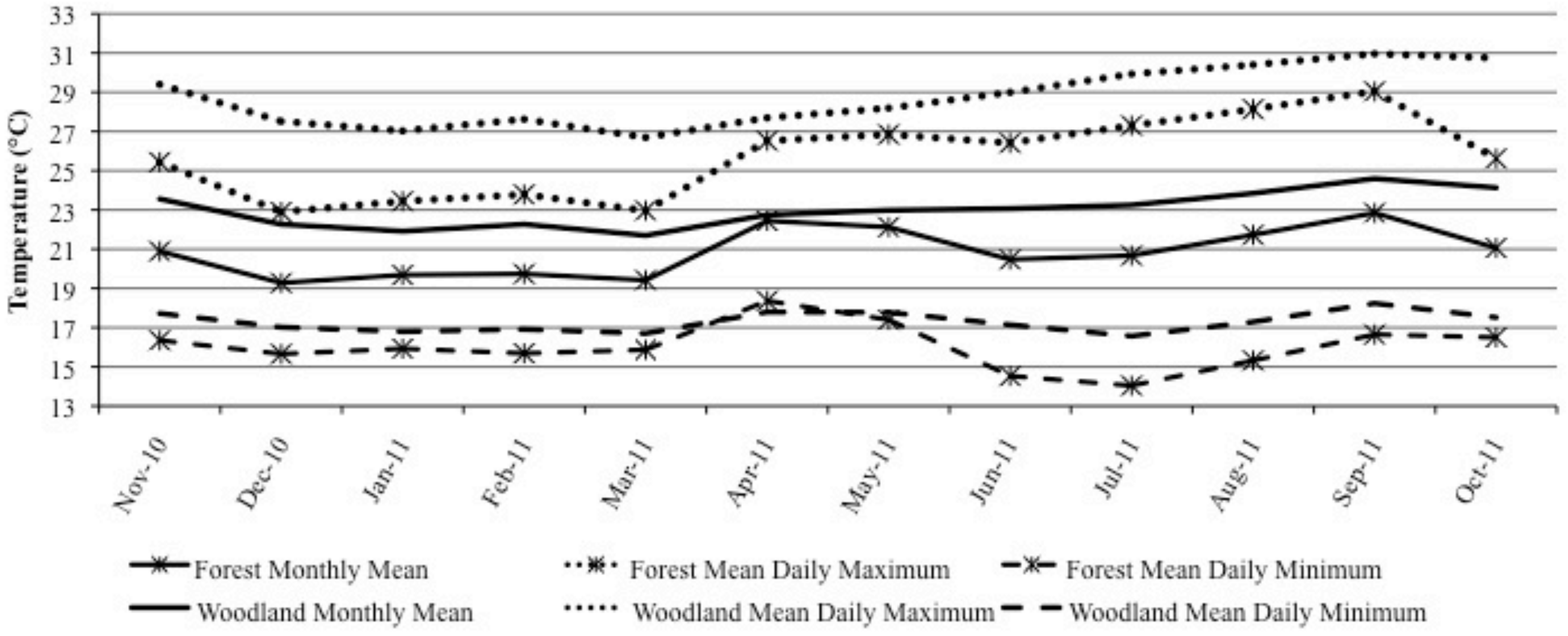


Figure 5-2. Monthly mean, mean daily maximum, and mean daily minimum temperature for forest and woodland in Issa.

RESOURCES

RESOURCE AVAILABILITY AND DISTRIBUTION

As stated in Chapter 3, the study site of Issa comprises less than two percent forest, which is mainly distributed along riverbeds in the valleys between woodland covered slopes. The 50 patch focals (12 forest and 38 woodland) used for behavioral observations also acted as vegetation plots, in which all stems with $\geq$5 cm DBH were measured.

The number of stems per patch ranged from 17 to 259, with both the least and most number of stems occurring in woodland patches. The number of stems in each patch was not necessarily correlated to the distribution of these stems; for example, some patches had few stems that were evenly distributed, while other patches had few stems that were clumped (i.e., not evenly distributed). Figure 5-3 provides examples of the appearance of these two types of distributions.

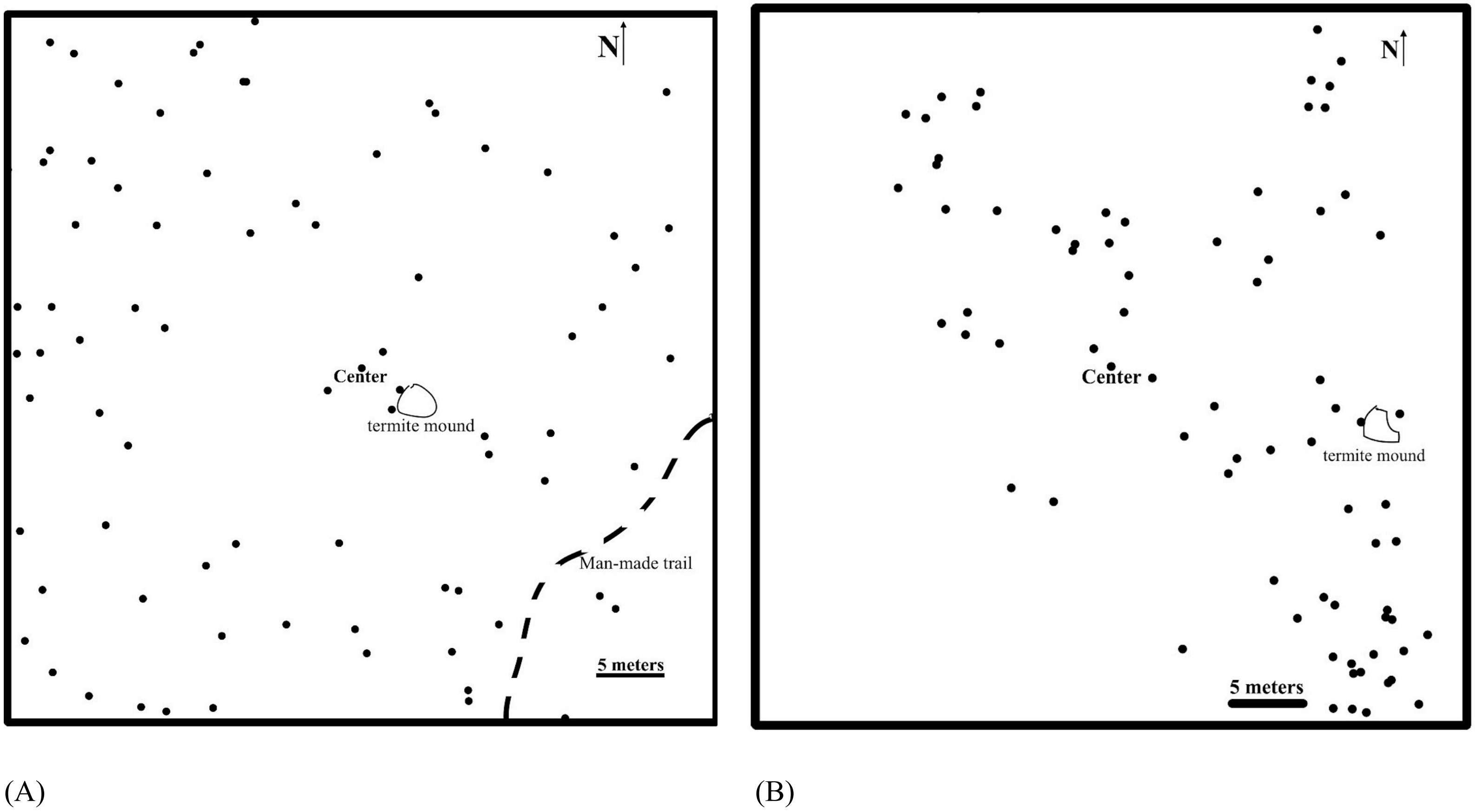


Figure 5-3. Representation of a patch with (A) an even distribution of stems [woodland patch P17] and (B) a clumped distribution of stems [woodland patch P41].

A total of 4571 stems were measured in the 50 patches located throughout the study site (see Chapter 4, Figure 4-1 for patch locations). Tables 5-1 and 5-2 list the total and average number of species, stems, and stem density measured in each habitat type. The total number of species measured for the entire study site includes some species that were found in both woodland and forest patches. A greater number of species were found in woodland patches, but it is important to remember that more areas of woodland were sampled as compared to forest, so this might simply be a sampling effect. When the number of patches sampled per habitat type is accounted for, there were more species, on average, in forest patches (Table 5-2). Similarly, the average number of stems was greater for woodland patches, but this might be an effect of patch size, as most woodland patches were $50m^2$ and most forest patches were $30m^2$. When patch size is accounted for, forest patches had a much higher density of stems.

Table 5-1
Total number of species, stems, and stem density present in 50 vegetation plots

Habitat	**Number of Species**	**Number of Stems**	**Density (stems/m^2)**
Woodland	151	3801	0.04
Forest	100	950	0.08
Total study site	217	4751	0.05

Table 5-2
Average number of species, stems, and stem density per patch, by habitat type

Habitat	**Average Number of Species/patch**	**Average Number of Stems/patch**	**Average Density (stems/m^2)/patch**
Woodland	3.97	100.03	0.001
Forest	8.33	79.17	0.006
Total study site	4.34	95.02	0.001

In addition to recording the species (if known) of each stem, the diameter at breast height (DBH) and height were also measured. Table 5-3 provides the descriptive statistics for these measured variables, in addition to maximum DBH for each habitat type. On average, woodland stems had larger DBH values than forest stems, but the largest DBH was recorded for a forest tree. Forest patches had mostly either small or very large stems, while woodland patches contained stems of all sizes. Forest stems were also, on average, taller than woodland stems, which is likely correlated to larger maximum DBH values (i.e., tall stems tend to have large DBH values).

Table 5-3
Descriptive statistics of measured variables for each habitat type

	Woodland	Forest
	DBH (cm)	
Mean	15.82	14.11
Median	11.10	9.00
Standard Deviation	11.88	14.32
Minimum	5.00	5.00
Maximum	101.90	146.20
Range	96.90	141.20
N	3801	950
	Maximum DBH (cm)	
Mean	60.90	85.41
Median	56.10	78.00
Standard Deviation	16.04	30.30
Minimum	38.80	46.30
Maximum	101.90	146.20
Range	63.10	99.90
N	38	12
	Height (m)	
Mean	24.25	34.23
Median	10.22	12.71
Standard Deviation	41.61	57.23
Minimum	1.68	1.72
Maximum	96.90	96.90
Range	95.22	95.18
N	3801	950

The ten most frequent species found in woodland and forest patches are given in Tables 5-4 and Table 5-5. The area of the study site is described as 'miombo' woodland, which is characterized by species of *Brachystegia*, *Julbernardia*, and *Isoberlinia*. Therefore, woodland patches dominated by species of *Brachystegia* were expected. Forest patches were dominated by *Julbernardia unijugata*, which also fits with previous classifications of the area. Similar frequencies of the species listed below were also found in a previous study (Hernandez-Aguilar, 2006), with differences attributed to variation in locations of vegetation plots and transects between this study and the previous one. A list of all plant species identified at Issa thus far (during this and previous studies) is presented in Appendix B.

Table 5-4
Frequency of ten most frequent species found in woodland patches. Numbers in parentheses represent the percentage out of total woodland stems sampled

Family	**Scientific Name**	**Frequency (percentage of total woodland stems)**
Fabaceae	*Brachystegia spiciformis*	705 (18.55%)
Fabaceae	*Brachystegia bussei*	619 (16.29%)
Fabaceae	*Brachystegia longifolia*	282 (7.42%)
Fabaceae	*Pterocarpus angolensis*	276 (7.26%)
Apocynaceae	*Diplorhynchus condylocarpon*	226 (5.95%)
Fabaceae	*Brachystegia utilis*	213 (5.60%)
Fabaceae	*Pterocarpus tinctorius*	107 (2.82%)
Fabaceae	*Pericopsis angolensis*	97 (2.55%)
Dipterocarpaceae	*Monotes* sp.*	86 (2.26%)
Annonaceae	*Artabotrys stolzii*	85 (2.24%)

*specimen is likely *M. glaber* or *M. elegans*, but identification is unconfirmed

Table 5-5
Frequency of ten most frequent species found in forest patches. Numbers in parentheses represent the percentage out of total forest stems sampled

Family	**Scientific Name**	**Frequency (percentage of total forest stems)**
Fabaceae	*Julbernardia unijugata*	310 (32.63%)
Sapindaceae	*Macphersonia gracilis*	57 (6.00%)
Clusiaceae	*Garcinia huillensis*	33 (3.47%)
Euphorbiaceae	*Drypetes gerrardii*	29 (3.05%)
Rutaceae	*Teclea nobilis*	26 (2.74%)
Sapindaceae	*Lecaniodiscus* sp.	23 (2.42%)
Ebenaceae	*Diospyros gabunensis*	22 (2.32%)
Annonaceae	*Artabotrys stolzii*	21 (2.21%)
Bignoniaceae	*Markhamia obtusifolia*	21 (2.21%)
Fabaceae	*Baphia descampsii*	21 (2.21%)

Vegetation is an important resource for both food and shelter, but the availability of other resources, such as alternative food items (e.g., insects, animal prey) and water sources are also of great significance. The presence of termite mounds inside patches was recorded, and it was found that 44 (out of 50) patches contained at least one termite mound. Furthermore, half of the patches had at least one large (greater than $1m^2$) termite mound, likely attributed to *Macrotermes*, a favorite food item of chimpanzees at other study sites. Various species of ants were also found throughout the study site, but not systematically sampled. The level of insectivory exhibited by chimpanzees at Issa is discussed, along with the rest of their dietary profile, in Chapter 6.

As mentioned in Chapter 3, most streams in the study area are seasonal and dry up during the dry season. Therefore, the water available for chimpanzees and other animals is limited to certain parts of the study area, especially during the dry season. Potential water sources in or near patches were noted, but further examination of water availability was not conducted during this study due to time constraints. A systematic study of water availability in both the wet and dry seasons is needed to fully understand how this aspect of the study site's ecology influences the behavior of chimpanzees and other fauna.

PHENOLOGY

The phenology results presented here represent the average relative abundance of plant parts for 50 vegetation plots/patches and three transects placed throughout the study site (Figures 5-4 to 5-7). For all figures, the abundance was scored as 0 to 5, with a 5 representing the maximum amount available. It should be noted that the abundance values shown on the y-axis are not the same for all graphs. The shaded grey areas represent the dry season during this study, lasting from April to September 2011.

The average relative abundance of mature leaves was higher in forest than in woodland for all months of the study period. Relative abundance of mature forest leaves began to decrease a few months into the dry season (June) and then increase again at the beginning of the wet season. Relative abundance of mature woodland leaves decreased at the beginning of the dry season (April), with a more pronounced decline than for forest. This pattern reflects the greater number of deciduous trees in woodland as compared with forest trees. These results are generally consistent with those of the only other phenological study done at Issa; Hernandez-Aguilar (2006) found a similar drop in relative abundance of mature woodland leaves as the dry season progressed (in her study, from June to September).

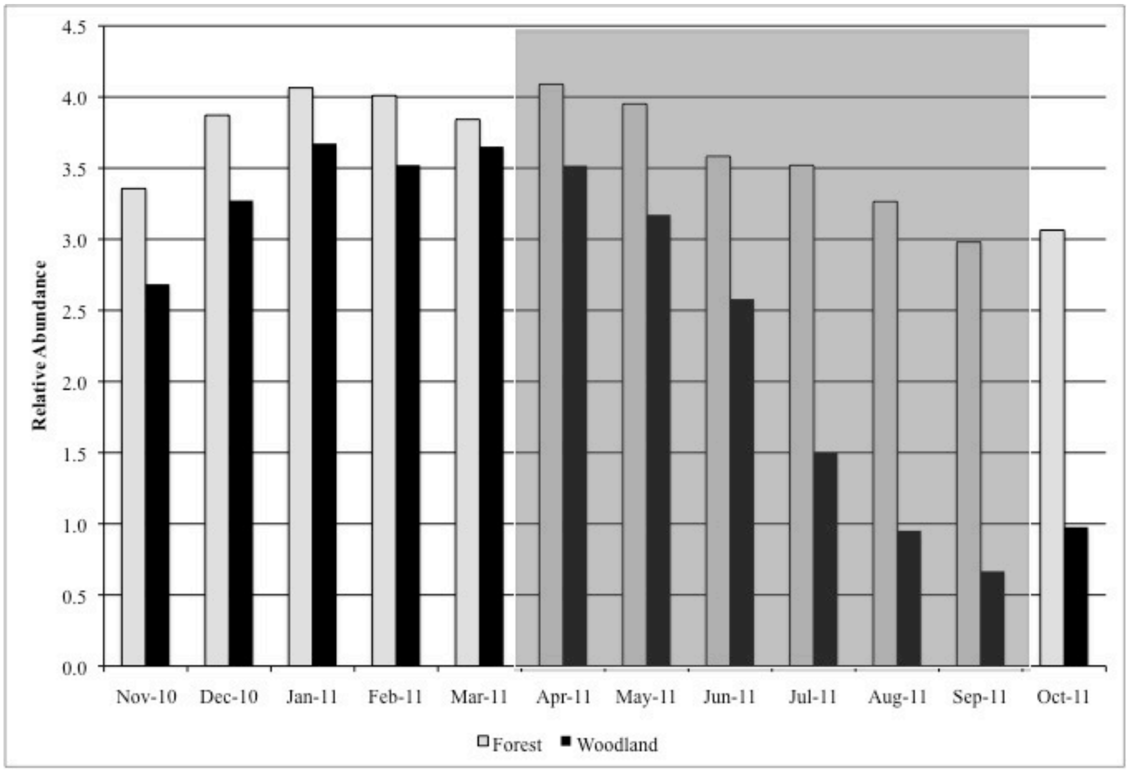


Figure 5-4. Relative abundance of mature leaves in forest and woodland. Shaded grey area represents the dry season.

The pattern of relative abundance of new leaves for forest was similar to that of mature leaves, in that there were no severe drops or peaks in abundance throughout the year. In contrast, the relative abundance of new woodland leaves decreased in the middle of the wet season, and began to increase in the middle of the dry season. Hernandez-Aguilar (2006) also found a peak in new woodland leaf abundance in August/September, at the end of the dry season.

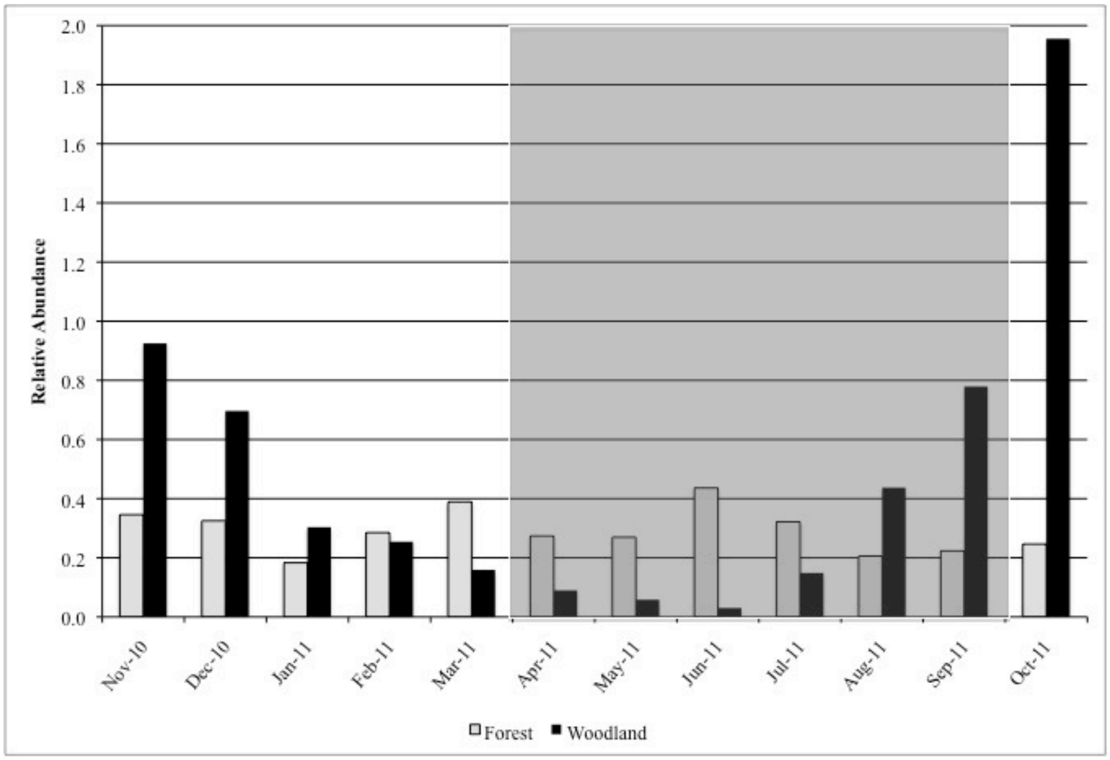


Figure 5-5. Relative abundance of young/new leaves in forest and woodland. Shaded grey area represents the dry season.

Overall, the relative abundance of flowers was low throughout the year in both forest and woodland; however, there was a greater abundance in woodland flowers for most of the months. For both habitat types, there was not a clear pattern in the timing of flower abundance, indicating that trees flower at various times throughout the year. Once again, these results match with those of the previous study, with woodland always having a higher abundance of flowers than forest (Hernandez-Aguilar, 2006).

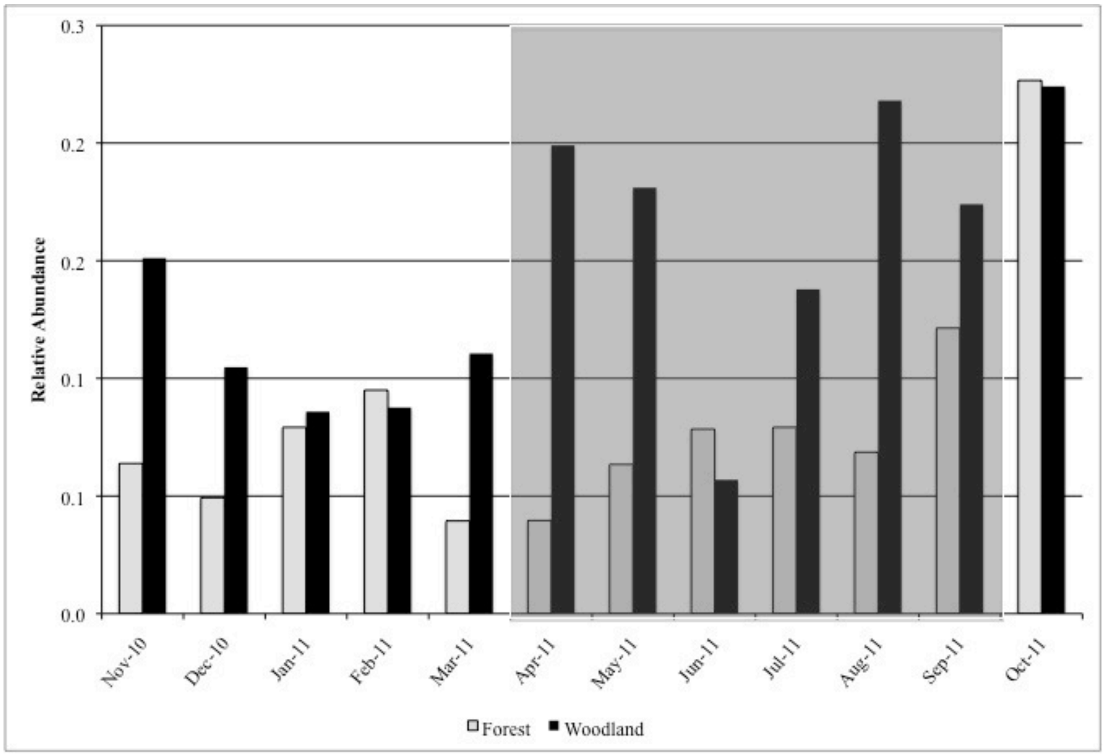


Figure 5-6. Relative abundance of flowers in forest and woodland. Shaded grey area represents the dry season.

While the relative abundance of fruits (including seeds and pods) was low in both woodland and forest throughout the year, there was never a complete absence of fruit. In all months, fruit abundance was higher in woodland than in forest; this pattern was also found in previous years (Hernandez-Aguilar, 2006). There were no extreme drops or peaks in fruit abundance throughout the year in forest, and only a slight drop in fruit abundance at the end of the dry season for woodland. This, like the pattern of flower abundance, reflects the range of timing in fruit production by trees in both habitat types.

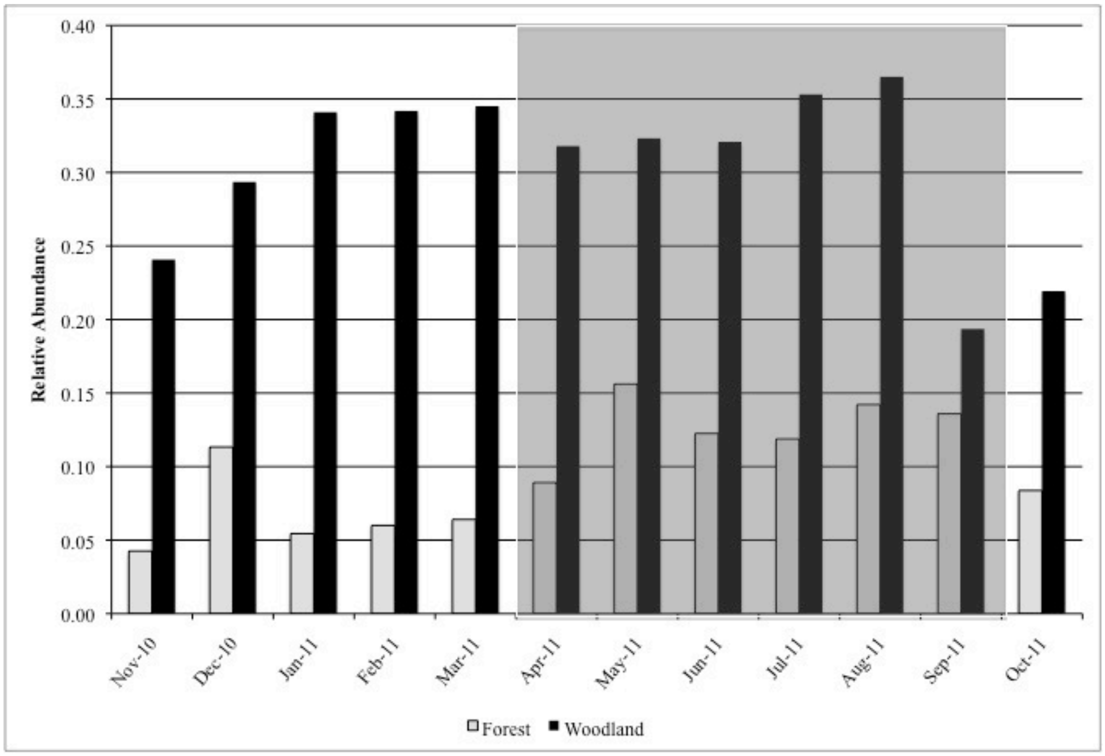


Figure 5-7. Relative abundance of fruits, seeds, and pods in forest and woodland. Shaded grey area represents the dry season.

DISCUSSION

The slight change in the temperature pattern of Issa between study periods is likely insignificant, but the change in annual rainfall and seasonality are extremely influential in altering the ecology of the site. A shift in the timing of rainfall throughout the year greatly influences the availability and distribution of food resources, which in turn, presents fauna with new challenges for finding food. At this time, it is unclear exactly how much of an effect these changing seasonality patterns have had on the fauna at Issa, as there are few data on resource availability and distribution from previous years. However, while the precise effects are currently unknown, there is no question that this shift in seasonality has affected the local ecology of the site, thus also affecting the behavior of fauna and people living in the area. For example, during this study period the river nearest to camp (which was relied upon for cooking, drinking, and bathing water) completely dried up, forcing me and the camp staff to bring in water from the town of Uvinza. While other smaller rivers in the study area have been known to go dry in the past, this particular river had never before run dry (as noted by locals, and beginning in 2001, by previous researchers). Fauna in the area would have also needed to go elsewhere for water, impacting foraging strategies and ranging behaviors.

Despite the more extreme conditions during this study period, food resources in the form of fruits/seeds/pods and leaves were available in all habitat types throughout the year. Therefore, it is likely that other factors, such as sloping terrain or the location of water, have a greater influence on animal behavior than the availability of fruit or leaves. Since it has been previously assumed that dry-habitat chimpanzee sites like Issa have limited resources, these results are especially important in re-evaluating researchers' notions about the ecology of such sites, and how this ecology influences animal behavior. The socio-ecological behavior of chimpanzees and other fauna at Issa are described in the following chapters, and a discussion of how the ecology and behavior of Issa fauna compares to the ecology and faunal behavior at other chimpanzee sites can be found in Chapter 8.

CHAPTER 6: RESOURCE USE BY ISSA CHIMPANZEES

The use of resources, particularly habitat space and food, is an important component of a species' niche, and greatly influences, and is influenced by, the use of resources by other fauna in the community. Therefore, before any community-wide patterns of resource use for Issa can be determined, habitat and dietary preferences for Issa chimpanzees first need to be established. Previous research at Issa includes the examination of nesting site preferences (Hernandez-Aguilar, 2006, 2009; Stewart, 2011; Stewart et al., 2011), but general patterns of habitat use have not yet been examined. Similarly, there is only limited information about dietary resources used by Issa chimpanzees; research conducted by Hernandez-Aguilar (2006, 2009) currently provides the only published data. Here, I discuss the results of my examination of resource use by Issa chimpanzees.

USE OF SPATIAL (HABITAT) RESOURCES

HABITAT PREFERENCE

Patterns of habitat use by Issa chimpanzees were determined based on the number of encounters in each habitat type, which consisted of woodland, forest, and grassland/swamp (90.5%, 1.5%, and 8% of the study site vegetation, respectively). However, no encounters were recorded for grassland/swamp during the study period, so only woodland and forest are compared here, and thus chimpanzee use of the entire habitat is limited to 92% of the total area. Encounters occurred both directly (i.e., direct visual observations and camera trap photos/videos) and indirectly (i.e., vocalizations and the presence of prints, feces, nests, and/or feeding remains). Independent encounters for all observations are defined in Chapter 4. Figure 6-1 shows the locations of all chimpanzee encounters during this study period.

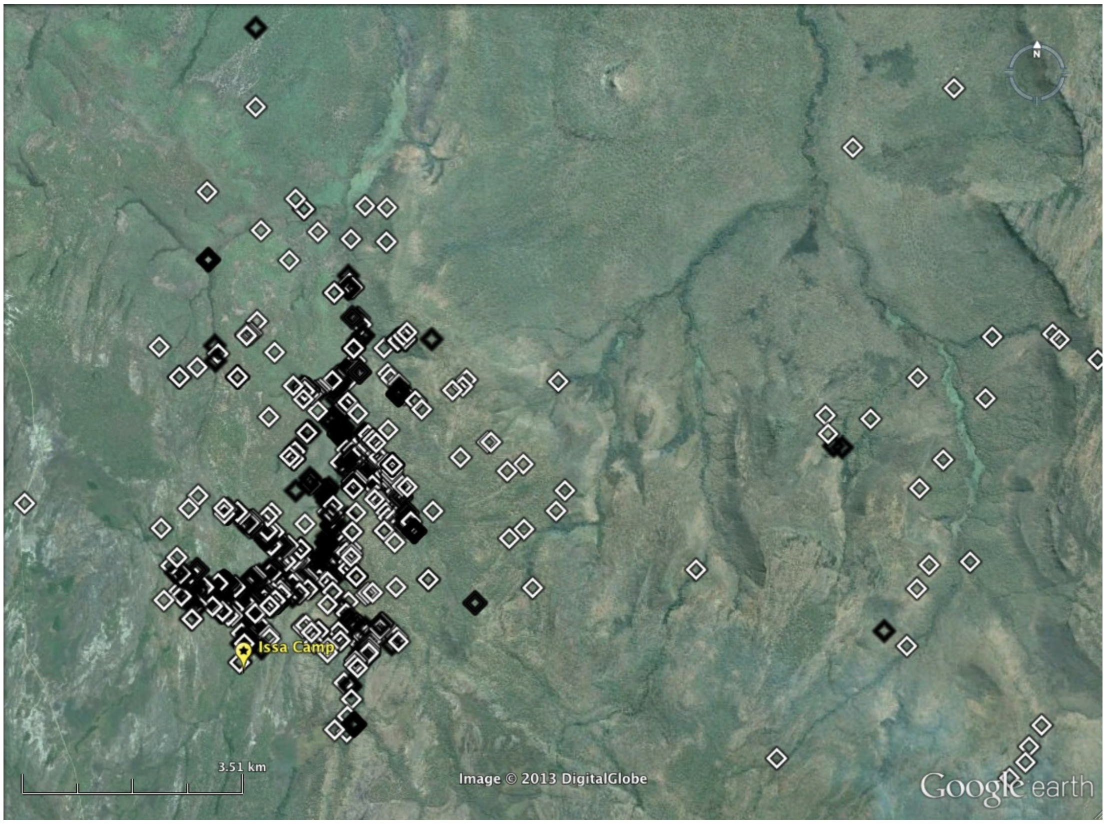


Figure 6-1. Distribution of all chimpanzee encounters during this study. Black diamonds represent observations in forest, white diamonds represent observations in woodland, and the yellow placemark represents camp.

Chimpanzees were directly observed in nine of the 50 (18%) patches located throughout the study site; of these, five were in forest habitat and four were in woodland. A total of 13 encounters were recorded, eight in forest habitat and five in woodland. At first glance these data appear to indicate that chimpanzees showed no selectivity in habitat use (for patches only). However, when availability of habitat type is taken into account (i.e., 38 (76%) woodland patches and 12 (24%) forest patches), there are significantly more encounters in forest patches than expected ($\chi^2 = 10.04$, n = 13, df = 1, p = 0.002; Table 6-1). This pattern of greater than expected forest encounters was true during the dry season only; the number of chimpanzee encounters in each habitat type during the wet season were no different than expected relative to habitat type (dry: $\chi^2 = 11.41$, n = 8, df = 1, p = 0.007; wet: $\chi^2 = 0.702$, n= 5, df = 1, p = 0.402).

It is important to note, however, that this statistical result might not be accurate due to small sample size. Therefore, in addition to those noted during patch focals, direct visual observations of chimpanzees were also recorded when traveling to or from patches and by field assistants when collecting data for other researchers. Moreover, 24 camera traps placed throughout the study site recorded direct observations. Therefore, these data were combined with patch focal data to increase the amount of potential habitat space in which chimpanzees could be observed (i.e., the entire study site as compared to patches only). These data show the same pattern as the patch focal data, with significantly more encounters in forest ($\chi^2 = 14970.2$, n = 366, df = 2, $p < 0.0001$; Table 6-1) relative to available habitat throughout the entire study area (i.e., 90.5% woodland, 1.5% forest, 8% grassland/swamp). Similar to the patch data, seasonal differences in habitat use were found; relative to habitat availability, a significantly higher number of chimpanzee encounters occurred in forest as compared to woodland in both the dry and wet seasons ($\chi^2 = 9048.3$, n = 223, df = 2, $p < 0.0001$; $\chi^2 = 5922.2$, n = 143, df = 2, $p < 0.0001$, respectively).

The occurrence of chimpanzees at a particular location was also indicated by indirect evidence, including vocalizations and the presence of feces, nests, prints, and/or feeding remains. These data exhibit the same pattern as that of all direct observations, with significantly more encounters in forest relative to habitat availability ($\chi^2 = 8183.37$, n = 871, df = 2, $p < 0.0001$; Table 6-1). Similarly, indirect evidence of chimpanzees was more prevalent in forest habitats as compared to woodland in both the dry and wet seasons ($\chi^2 = 5353.3$, n = 481, df = 2, $p < 0.0001$; $\chi^2 = 2909.6$, n = 390, df = 2, $p < 0.0001$, respectively).

When all data sources (i.e., direct observations and indirect evidence) are combined, the pattern of significantly more use of forest relative to its availability is maintained ($\chi^2 = 20282.61$, n = 1237, df = 2, $p < 0.0001$), again with no seasonal differences (dry: $\chi^2 = 12993.5$, n = 704, df = 2, $p < 0.0001$; $\chi^2 = 7389.2$, n = 533, df = 2, $p < 0.0001$, respectively). Table 6-1 summarizes the results from the analyses of each dataset used in this study. In sum, when habitat availability is accounted for, Issa chimpanzees are using forest much more than expected, throughout both the dry and wet seasons (Figure 6-2).

Table 6-1

Summary of Issa chimpanzee habitat use relative to habitat availability

	Woodland encounters	**Forest encounters**	χ^2	**df**	**p**	**Seasonal difference?**
Patch focals only*	5	8	10.04	1	0.002	Yes (dry season only)
All direct observations	76	290	14970.2	2	<0.0001	Yes
Indirect data only	534	337	8183.37	2	<0.0001	Yes
All data (direct and indirect observations)	610	627	20282.61	2	<0.0001	Yes

*Habitat availability for patch focals differs from that for other data (76% woodland and 24% forest for patches versus 90.5% woodland, 1.5% forest, 8% grassland/swamp for all other data)

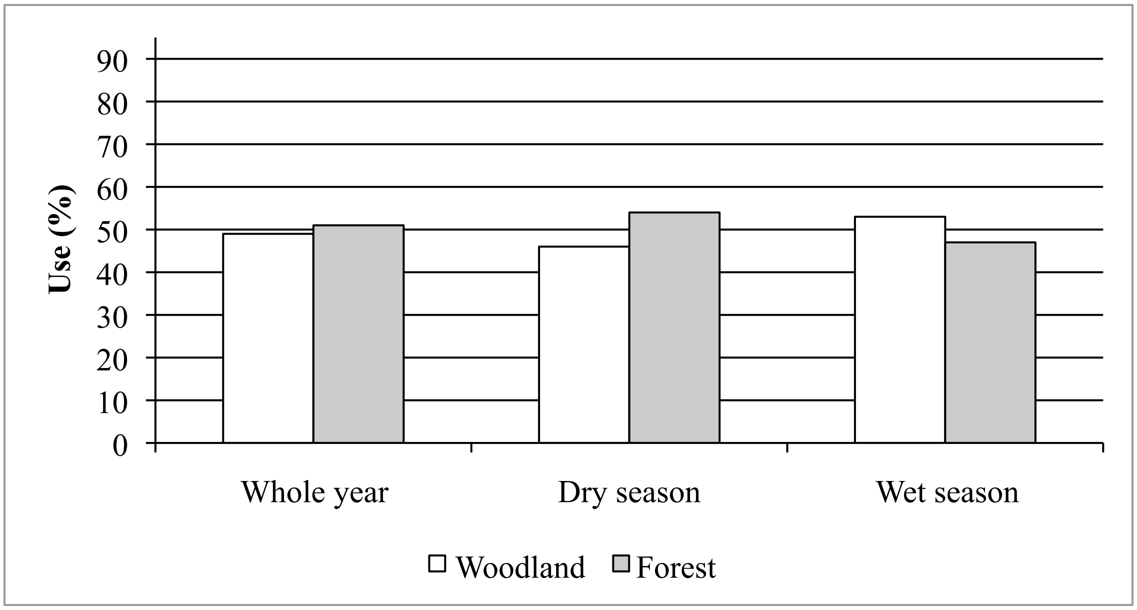


Figure 6-2. Percent of habitat use by Issa chimpanzees based on all data sources.

While the previous analyses show no seasonal differences in habitat use relative to habitat availability, an interesting seasonal pattern of use became apparent when examining chimpanzee use within each of the habitat types. Of the total number of chimpanzee encounters occurring in forest habitat only (from all data sources, n = 627), more took place during the dry season as compared to the wet season (dry n = 378, wet n = 249; $\chi^2 = 26.5$, df = 1, $p < 0.0001$). In contrast, chimpanzee encounters in woodland habitat only (from all data sources, n = 610) took place during both the dry and wet seasons equally (dry n = 326, wet n = 284; $\chi^2 = 2.9$, df = 1, p = 0.09). These patterns likely associate with the increased need of chimpanzees for water and shade during the dry season, which would be found more in forest as compared woodland habitat.

BEHAVIOR ACROSS HABITAT TYPES

During patch focals, the behaviors of chimpanzees present were recorded as travel, rest, or eat. Due to a small number of encounters in patches, behavioral data recorded during observations of chimpanzees outside of patches were also included in the analyses. However, these data were not recorded in a systematic or consistent manner. Therefore, analyses were conducted on both datasets: patch focals only and all direct observations (not including camera trap photos/videos). Additionally, data were analyzed based on both encounters and total time observed in each habitat type.

During a total of 13 encounters in patches, chimpanzees were traveling in 77% (n = 10), resting in 16% (n = 2), and eating in 7% (n = 1). Traveling occurred more often in forest than woodland, but resting occurred equally in each habitat type, and eating was only observed in woodland patches (Figure 6-3). Including data from non-patches gives similar results, with chimpanzees traveling in 76% (n = 263), resting in 14% (n = 49), and eating in 10% (n = 33) of all encounters (Figure 6-4). There are, however, slight differences in how these behaviors are distributed across habitat types. Chimpanzees were still observed travelling more in forest than woodland, but rested more in forest, and were observed eating an equal amount of times in each habitat.

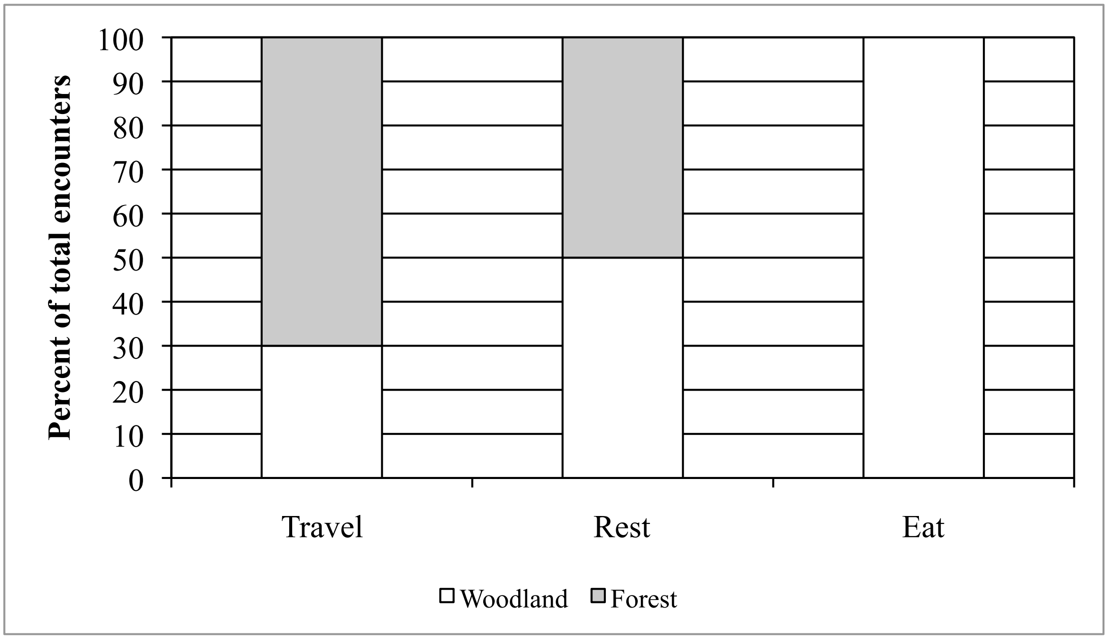


Figure 6-3. Behavior of Issa chimpanzees in patches, based on encounters (travel n = 10, rest n = 2, eat n = 1, total n = 13).

Figure 6-4. Behavior of Issa chimpanzees throughout the study site, based on encounters (travel n = 263, rest n = 49, eat n = 33, total n = 345).

Behaviors were also distributed differently within habitat types. In both woodland and forest habitats, chimpanzees were travelling during most encounters, but the distribution of resting and eating differed. Issa chimpanzees were encountered resting and eating about an equal number of times in woodland, but were observed to rest more often than eat when in forest habitat (Figure 6-5).

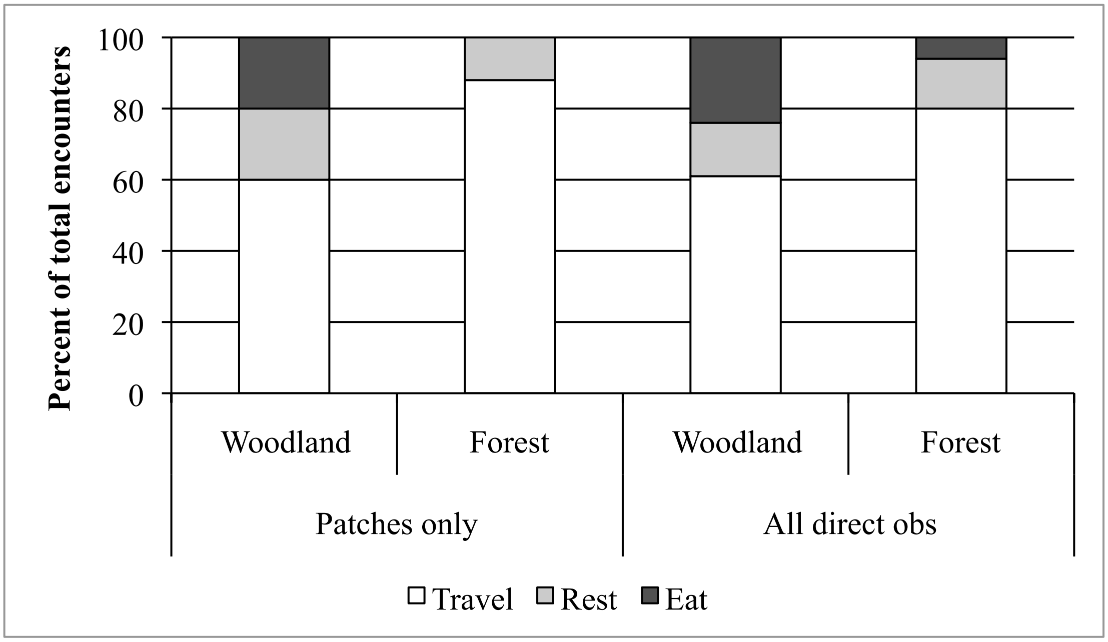


Figure 6-5. Behavior of Issa chimpanzees within each habitat type, based on encounters (patches only: woodland n = 5, forest n = 8, all direct observations: woodland n = 66, forest n = 279).

When looking at the duration of these behaviors, a slightly different picture emerges. Of the total time observed when in patches (28.2 minutes), chimpanzees still spent most of their time travelling (60%), but also spent a large amount of time resting (33%), and the least amount of time eating (7%). Chimpanzees spent an equal amount of time travelling in both woodland and forest patches, but spent more time resting and eating in woodland (Figure 6-6). Including additional data from outside patches continues to skew the picture, with chimpanzees eating 58% of the total time observed (1021 minutes), resting 35% of the total time, and traveling only 7% of the total time. More time was spent travelling in woodland than forest, but more time was spent resting and eating in forest than woodland (Figure 6-7).

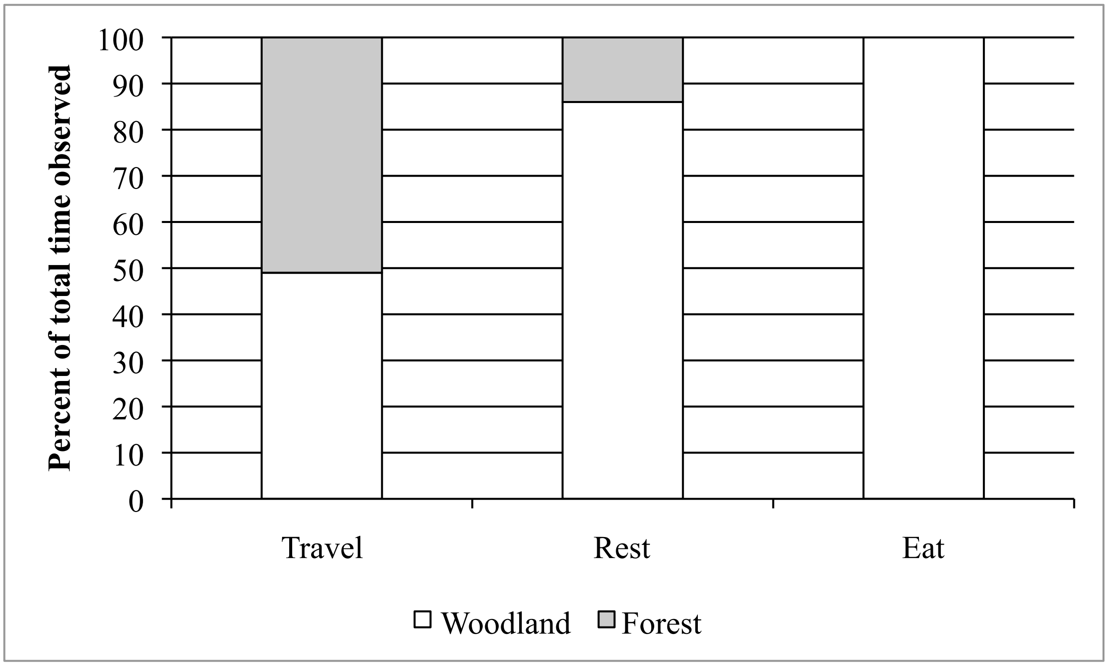


Figure 6-6. Behavior of Issa chimpanzees in patches, based on total time observed (travel = 16.85 min, rest = 9.33 min, eat = 2 min, total = 28.2 minutes).

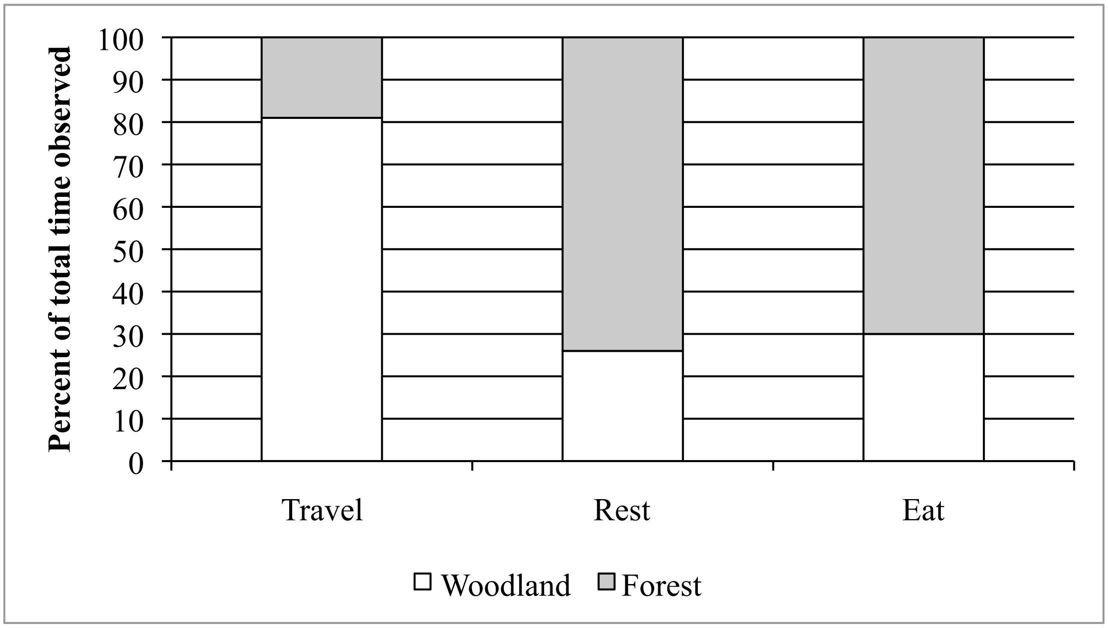


Figure 6-7. Behavior of Issa chimpanzees throughout the study site, based on total time observed (travel = 71.35 min, rest = 354.33 min, eat = 595.5 min, total = 1021 minutes).

The distribution of time spent traveling, resting, or eating within a particular habitat type is presented in Figure 6-8. During their time spent in woodland patches only, chimpanzees travelled and rested a similar amount of time, and spent the least amount of time eating. Chimpanzees were never observed to eat when in forest patches, and spent a much greater amount of time traveling than resting. When all direct observations are considered, chimpanzees appear to spend most of their time eating, followed by resting and then traveling in both woodland and forest habitat.

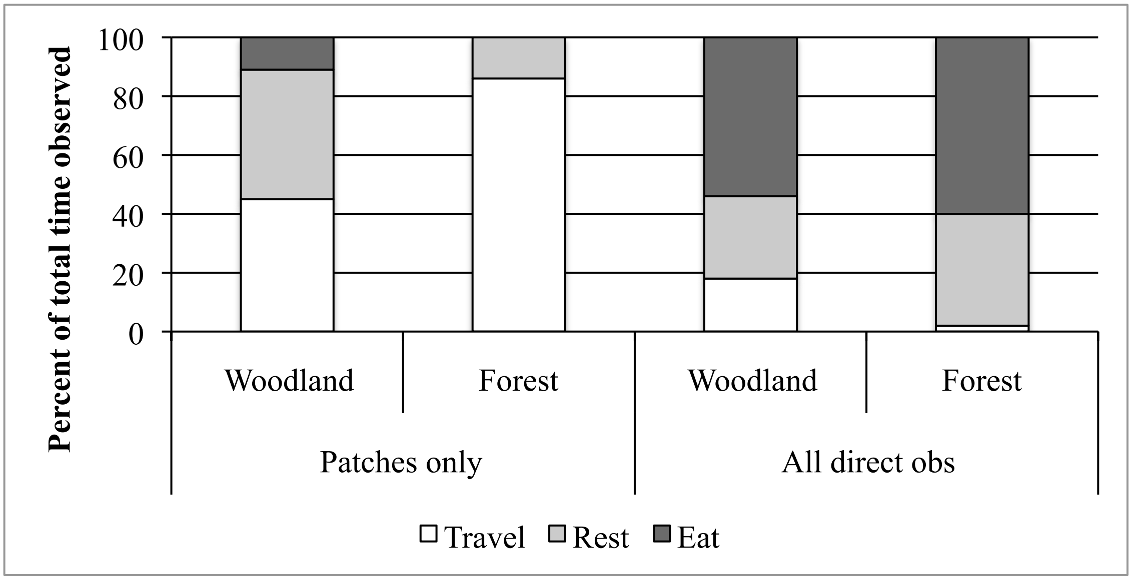


Figure 6-8. Behavior of Issa chimpanzees within each habitat type, based on total time observed (patches only: woodland = 18.34 min, forest = 9.84 min; all direct observations: woodland = 326.34 min, forest = 694.84 min).

Overall, it can be concluded that chimpanzees are most often observed while travelling in comparison to resting or eating. This is not surprising as their movement can make them easier to locate and observe, as compared to when they are quietly resting. Furthermore, chimpanzees at Issa have a large home range (Hernandez-Aguilar, 2006, 2009; Stewart, 2011; Stewart et al., 2011; Piel and Stewart, unpublished data), so much of their time is spent moving throughout their environment. The increase in time spent eating based on all direct observations as compared to data from patches in Figure 6-7 and 6-8 is likely due to a bias in data collection; outside of patches, field assistants often recorded the duration of feeding events, but often neglected to note the duration of any travelling observed. Therefore, a conclusion about whether Issa chimpanzees spend more time resting or eating cannot be made at this time. In addition, there does not appear to be a bias in behavior relative to habitat type, but more behavioral observations are needed before a final conclusion can be reached.

USE OF DIETARY (FOOD) RESOURCES

Direct observations of feeding behavior of Issa chimpanzees were limited in number; chimpanzees were observed eating during patch focals only once and observed feeding outside of patch locations a total of 21 times on 17 different plant species (Table 6-2). Additional dietary data came from feeding remains located throughout the study area (Figure 6-9). However, observational and feeding remains data only represent a small subset of the diet of Issa chimpanzees, so all analyses presented here were performed on data from fecal samples only, and not from direct observations.

Table 6-2

Plant species and part eaten by Issa chimpanzees from direct observations

Family	**Species**	**Part eaten**	**Habitat**
Annonaceae	*Monanthotaxis poggei*	fruit	Forest
Apocynaceae	*Saba comorensis*	fruit	Forest
Apocynaceae	Unknown liana	fruit	Forest
Boraginaceae	*Cordia* sp.	fruit	Forest
Clusiaceae	*Garcinia huillensis*	fruit	Forest/Woodland
Fabaceae	*Brachystegia spiciformis*	fruit	Woodland
Fabaceae	*Brachystegia utilis*	fruit, new leaves	Woodland
Fabaceae	*Julbernardia unijugata*	fruit	Forest
Fabaceae	*Pterocarpus tinctorius*	fruit, flowers, new leaves	Woodland
Loganiaceae	*Strychnos innocua*	fruit	Woodland
Moraceae	*Ficus exasperata*	fruit	Forest/Woodland
Moraceae	*Ficus variifolia*	fruit	Forest/Woodland
Myrtaceae	*Syzygium guineense*	fruit	Woodland
Olacaceae	*Ximenia caffra*	fruit	Woodland/Wooded Grassland
Rubiaceae	*Psychotria* sp.	fruit	Forest/Woodland
Sapindaceae	*Zanha africana*	fruit	Woodland
Verbenaceae	*Vitex doniana*	fruit	Woodland

(a) (b)

Figure 6-9. Chimpanzee feeding remains: (a) *Psychotria* sp. wadge and (b) evidence of cambium scraped from *Brachystegia bussei* bark.

A total of 297 fecal samples were collected throughout the study period, and analyzed for content, as described in Chapter 4; of these, 225 samples were collected during the dry season and 72 samples were collected during the wet season. Of the total samples analyzed, 294 samples (99%) contained at least one kind of seed and 164 samples (55.4%) contained *Ficus* sp. seeds. On average, the presence of seeds in each sample represented three different plant species, with a maximum amount of eight different plant species. This pattern was consistent throughout both the dry and wet seasons. The presence of *Ficus* sp. was less prevalent in samples collected during the wet season (47%) than those collected during the dry season (58%), though this difference was not significant (t-value: -1.566, p = 0.12). Chewed greens were present in 56 samples (18.9%), and were equally prevalent in both the dry and wet season (19%). Invertebrates were only found in 27 samples (9.1%), and significantly found more during the wet season (25%) than the dry season (10%; t-value: 2.693, p = 0.008). There were no vertebrate remains found in any fecal samples collected.

During this study, 98 different seeds (i.e., plant species) were identified among fecal samples, but previous research includes 55 additional plant species that comprise the diet of Issa chimpanzees, for a total of 153 species identified thus far (this study, Hernandez-Aguilar 2006, 2009; Piel and Stewart, unpublished data; Appendix B). Of these 153 plant species, 79 have been given habitat classifications; 28% occur in forest, 47% in woodland, 11% in forest/woodland, 13% in woodland/wooded grassland, and 1% in wooded grassland. Table 6-3 gives the ten most frequently consumed plant species found during this study, and their habitat classifications.

Table 6-3
Most frequent plant species consumed by chimpanzees during this study, from fecal analyses

	Family	Species	% of total samples	Habitat
Whole year				
	Boraginaceae	*Cordia* sp.	29.7%	Forest
	Zingiberaceae	*Aframomum mala*	18.2%	Forest/Woodland/Wooded Grassland
	Flacourtiaceae	*Flacourtia indica*	16.6%	Forest
	Tiliaceae	*Grewia rugosifolia*	13.2%	Woodland
	Unknown	Unknown seed #57	12.8%	Unknown
	Verbenaceae	*Vitex doniana*	12.2%	Woodland
	Clusiaceae	*Garcinia huillensis*	11.8%	Forest/Woodland
	Annonaceae	*Annona senegalensis*	11.1%	Woodland
	Apocynaceae	*Saba comorensis*	10.8%	Forest
	Unknown	Unknown seed #58	10.8%	Unknown
Dry season				
	Boraginaceae	*Cordia* sp.	38.2%	Forest
	Zingiberaceae	*Aframomum mala*	24.0%	Forest/Woodland/Wooded Grassland
	Flacourtiaceae	*Flacourtia indica*	19.1%	Forest
	Unknown	Unknown seed #57	16.9%	Unknown
	Verbenaceae	*Vitex doniana*	16.0%	Woodland
	Tiliaceae	*Grewia rugosifolia*	14.7%	Woodland
	Unknown	Unknown seed #58	14.2%	Unknown
	Annonaceae	*Annona senegalensis*	11.6%	Woodland
	Myrtaceae	*Syzygium guineense*	9.8%	Woodland
	Vitaceae	*Ampelocissus obtusata*	9.3%	Forest
Wet season				
	Apocynaceae	*Saba comorensis*	47.9%	Forest
	Clusiaceae	*Garcinia huillensis*	46.5%	Forest/Woodland
	Annonaceae	*Uvaria angolensis*	19.7%	Forest
	Unknown	Unknown seed #38	14.1%	Unknown
	Annonaceae	*Annona senegalensis*	9.9%	Woodland
	Loganiaceae	*Strychnos cocculoides*	9.9%	Forest
	Tiliaceae	*Grewia rugosifolia*	8.5%	Woodland
	Anisophylleaceae	*Anisophyllea boehmii*	8.5%	Woodland
	Flacourtiaceae	*Flacourtia indica*	8.5%	Forest

The diet of Issa chimpanzees varied throughout the year, likely reflecting the availability of different fruit resources in the dry and wet seasons. However, there are no clear patterns of habitat use based on diet; chimpanzees frequently fed on plants found in both forest and woodland. Of the plant species listed above in Table 6.3, only one species, *Garcinia huillensis*, was also one of the most prevalent species found during phenological transects for this study (Chapter 5, Table 5-5). Hernandez-Aguilar (2006) found this species, in addition to *Vitex doniana, Annona senegalensis,* and *Syzygium guineense*, to occur frequently along transects. Along transects from this and previous studies, all other species were found rarely or not at all. Therefore, it is clear that the diet of Issa chimpanzees is not restricted by the availability of particular plant species, as preferred food items are not necessarily the most prevalent species within the study area.

DISCUSSION

Chimpanzees at Issa were encountered more often in forest than expected relative to habitat availability. When habitat availability is overlooked, chimpanzees only showed a slight selectivity for forest as compared to woodland during the dry season. This pattern does not seem to be influenced by the availability of food resources, as chimpanzees consumed items from plant species found in both forest and woodland habitats throughout the year. Furthermore, the phenological data presented in Chapter 5 showed that fruit was available throughout the year, and always more abundant in woodland than in forest. It is more likely that the availability of water is driving this pattern of habitat use; during the dry season almost all rivers in the area go dry, leaving only small pools of water within the riverbeds. These riverbeds are all located in the middle of forest habitats, so the chimpanzees would benefit from staying in forested habitats to be nearer to water sources and increased shade, especially during the dry season.

In general, the activity patterns exhibited by Issa chimpanzees during this study are similar to behavioral patterns found by previous researchers. Stewart (2011) and Hernandez-Aguilar (2006, 2009) both found chimpanzees to extensively use woodland habitat for travel, feeding, and nesting. Hernandez-Aguilar (2006) suggested that for Issa chimpanzees, the presence of tall trees (used for feeding and nesting), regardless of habitat type, is the important factor in determining chimpanzee ranging behavior. Therefore, the lack of habitat preferences for particular behaviors is not unexpected.

Similar to other chimpanzee communities, the diet of Issa chimpanzees consists mostly of fruit, with leaves comprising a smaller percentage of their diet. The presence of *Ficus* seeds in a little over half of the fecal samples collected suggest that this species is an important food resource for Issa chimpanzees despite its low density throughout the study area (Hernandez-Aguilar, 2006, 2009). However, there were no seasonal differences in consumption of *Ficus* and this species was eaten even when other foods were available, indicating that this species is not a fallback food for Issa chimpanzees; this contrasts the assertion by other researchers that figs are important fallback foods for chimpanzees (e.g., Wrangham et al., 1996).

Another interesting aspect of the dietary profile of Issa chimpanzees is the absence of evidence of hunting. However, this is not surprising as no previous evidence (e.g., direct observations, hair/bone in feces) have been recorded. Furthermore, it has been shown that while food resources are abundantly available at Issa (this study; Hernandez-Aguilar, 2006), these resources are spread out throughout the study area causing chimpanzees to have to range far to find food. Therefore, the time and energy required for hunting are not available to Issa chimpanzees. With that said, hunting by chimpanzees is a rare event in general, so it is also possible that hunting events occur at Issa, but have simply not yet been observed. A lack of extra time and energy might also explain the minimal amount of insectivory evidenced by remains in fecal samples. Insects like ants and termites are quite abundant at Issa, but chimpanzees have been observed to termite-fish only a handful of times over the past 10 years of research in the area. However, a systematic study of insectivory at Issa has yet to be conducted, so it is possible that the results from this study underestimate the degree of insectivory exhibited by Issa chimpanzees.

Since chimpanzees at Issa appear to use spatial and dietary resources equally in both woodland and forest, they are exposed to a large number of other fauna that use resources from both of these habitat types. This greatly increases the number of potential competitors that chimpanzees interact with, which can influence their ranging and feeding behaviors. The extent of interspecific competition for spatial and dietary resources is discussed in the next chapter.

CHAPTER 7: COMMUNITY ECOLOGY OF ISSA FAUNA

As previously mentioned, the ecological role of chimpanzees is greatly influenced by the presence and behaviors of the other animals with which they share their resources. However, not much is known about the faunal community at Issa besides presence/absence of particular species, and even then, this information is incomplete (see Table 3-2 and Appendix A). Therefore, the community ecology of Issa fauna, particularly use patterns of both spatial and dietary resources, was examined.

For the following analyses and results, animals were categorized into the following groups: artiodactyls (“A”, e.g., bushbuck, bushpig, duikers, hartebeest, antelopes); birds of prey (“B”, e.g. hawks, eagles); carnivores (“C”, e.g., hyena, leopard, lion, jackal); frugivorous birds (“FB”, e.g., turaco, parrot, hornbill); herpestids (“H”, e.g., mongoose species); non-chimpanzee primates (“NCP”, e.g., redtail monkey, vervet, baboon); rodents (“R”, e.g., squirrel, porcupine); and others (“O”, e.g., hyrax, genet, elephant shrew). A complete list of animal species within each category is given in Appendix A.

USE OF SPATIAL (HABITAT) RESOURCES

HABITAT PREFERENCE

The number of encounters of each animal species in a particular habitat type (i.e., woodland, forest, or grassland/swamp) was used to determine patterns of habitat use by Issa fauna. As described in previous chapters, encounters occurred both directly and indirectly. For direct observations, an independent encounter was defined as the observation of one or more individuals of a particular species in a distinct location, in which no individuals of this same species had been previously observed within the prior five minutes. This interval was increased to 30 minutes for camera trap photos/videos (see Chapter 4 for explanation). Indirect encounters were considered independent when occurring in a location not previously recorded on that same day.

A total of 789 independent encounters of non-chimpanzee fauna were recorded during patch focals. Of these, 607 (77%) occurred in woodland patches and 182 (23%) occurred in forest patches. This distribution of encounters is what would be expected relative to the availability of patch habitat types (i.e., 76% woodland patches vs. 24% forest patches; $\chi^2 = 0.3764$, df = 1, p = 0.54). Combining all data sources, a total of 6,418 independent encounters of non-chimpanzee fauna were recorded throughout the study area. Figures 7-1 to 7-7 depict the distribution of all non-chimpanzee faunal encounters during this study.

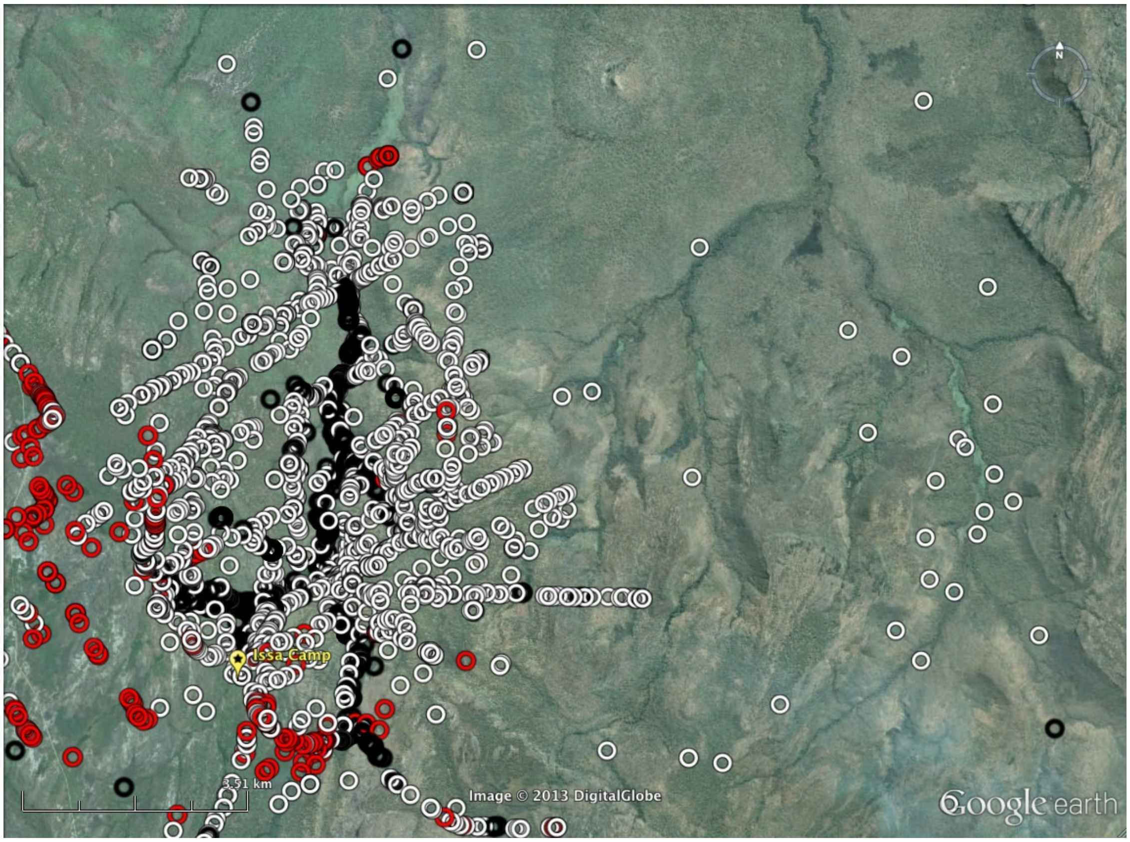


Figure 7-1. Distribution of all artiodactyl encounters during this study. Red circles represent encounters in grassland/swamp, black circles represent encounters in forest, white circles represent encounters in woodland, and the yellow placemark represents camp.

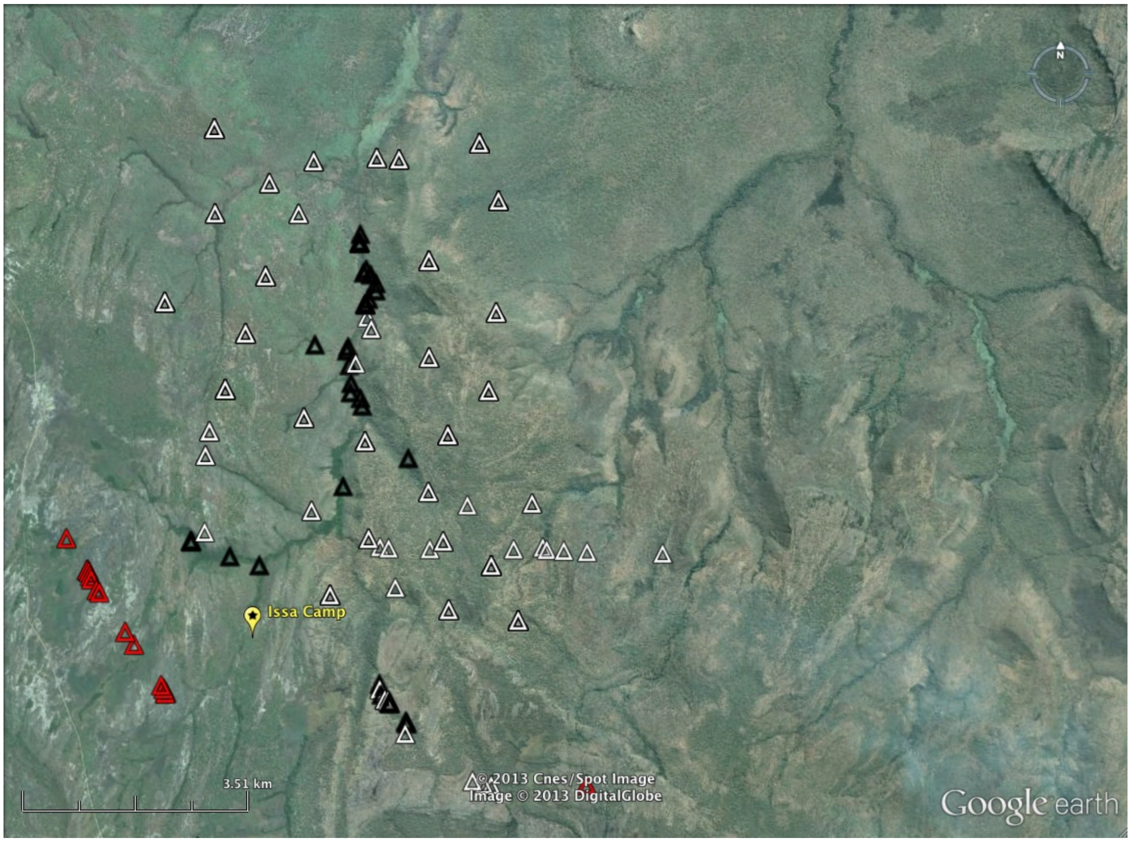


Figure 7-2. Distribution of all bird of prey encounters during this study. Red triangles represent encounters in grassland/swamp, black triangles represent encounters in forest, white triangles represent encounters in woodland, and the yellow placemark represents camp.

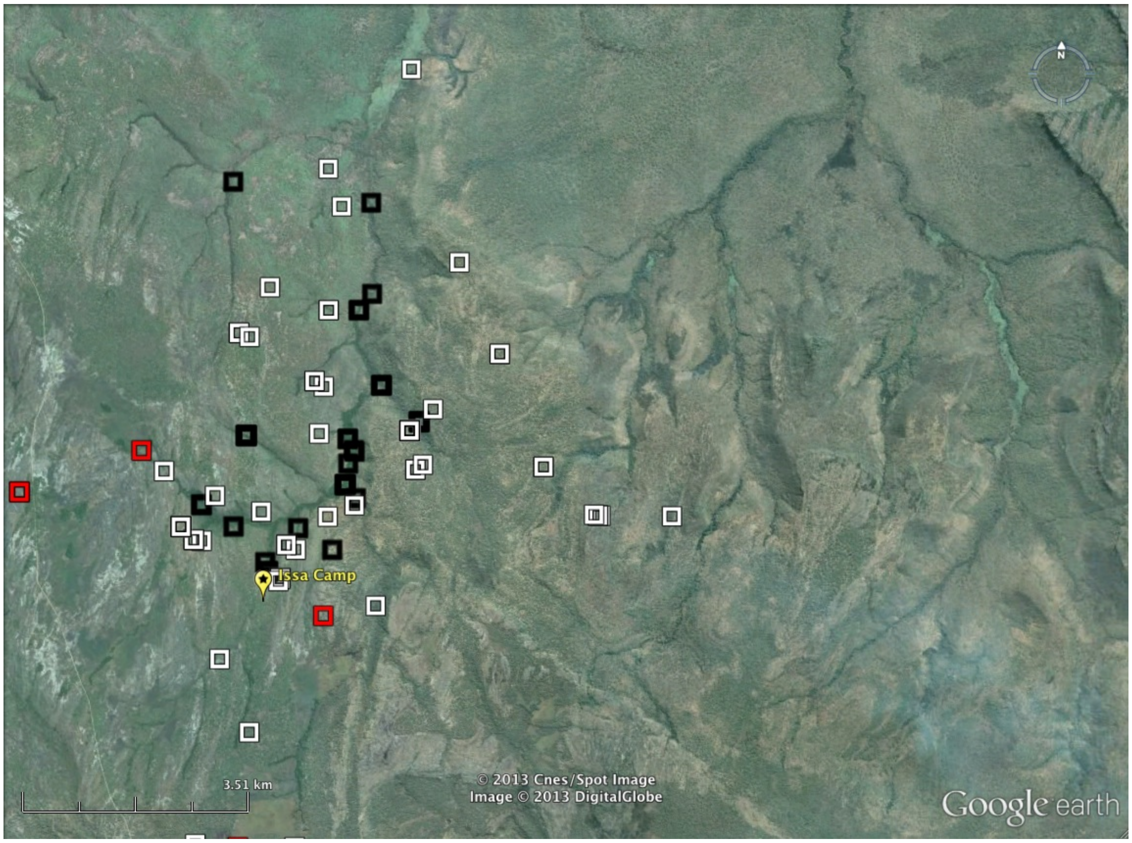


Figure 7-3. Distribution of all carnivore and herpestid encounters during this study. Red squares represent encounters in grassland/swamp, black squares represent encounters in forest, white squares represent encounters in woodland, and the yellow placemark represents camp.

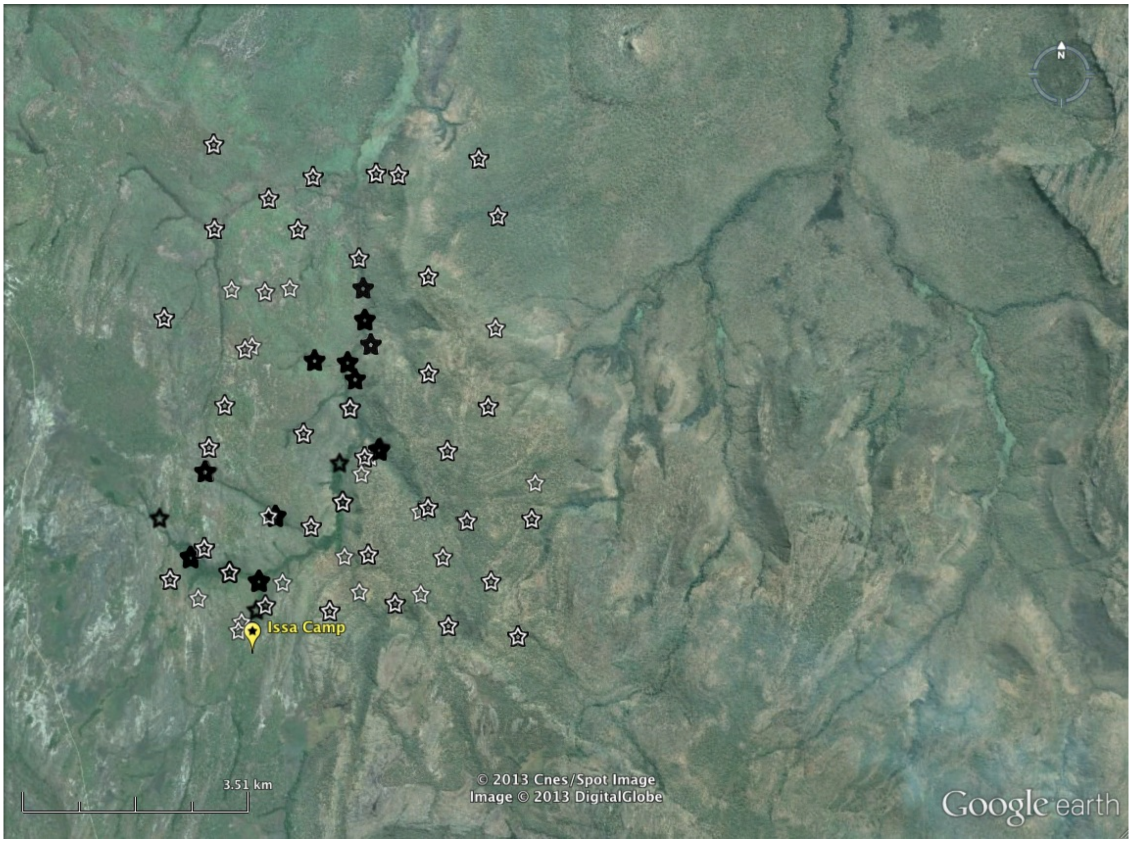


Figure 7-4. Distribution of all frugivorous bird encounters during this study. Black stars represent encounters in forest, white stars represent encounters in woodland, and the yellow placemark represents camp.

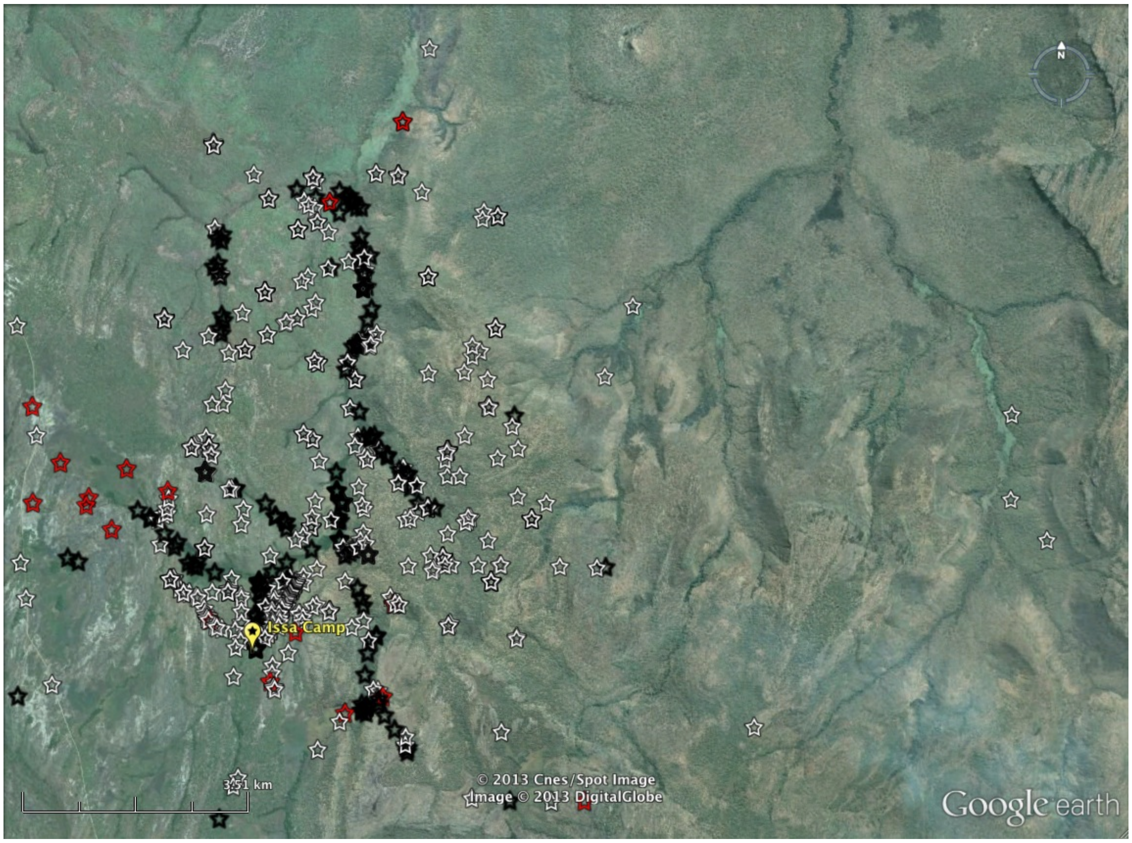


Figure 7-5. Distribution of all non-chimpanzee primate encounters during this study. Red stars represent encounters in grassland/swamp, black stars represent encounters in forest, white stars represent encounters in woodland, and the yellow placemark represents camp.

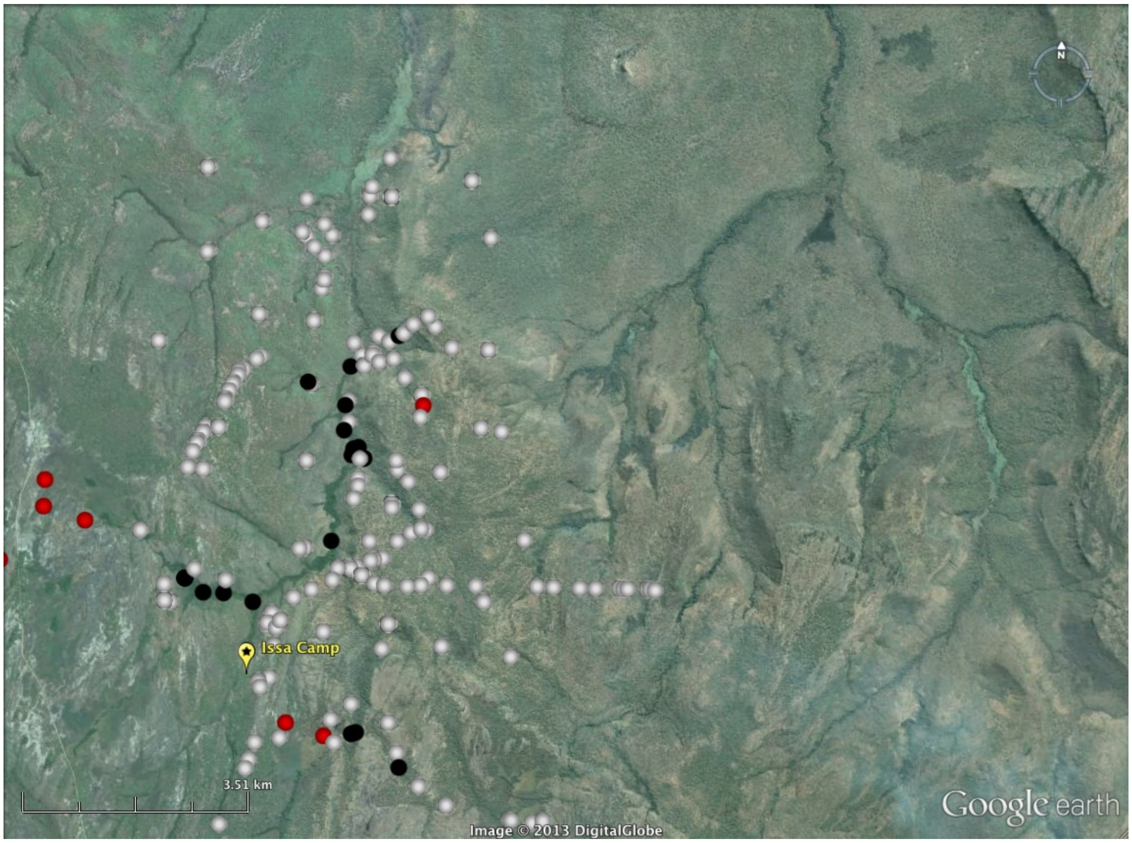


Figure 7-6. Distribution of all rodent encounters during this study. Red dots represent encounters in grassland/swamp, black dots represent encounters in forest, white dots represent encounters in woodland, and the yellow placemark represents camp.

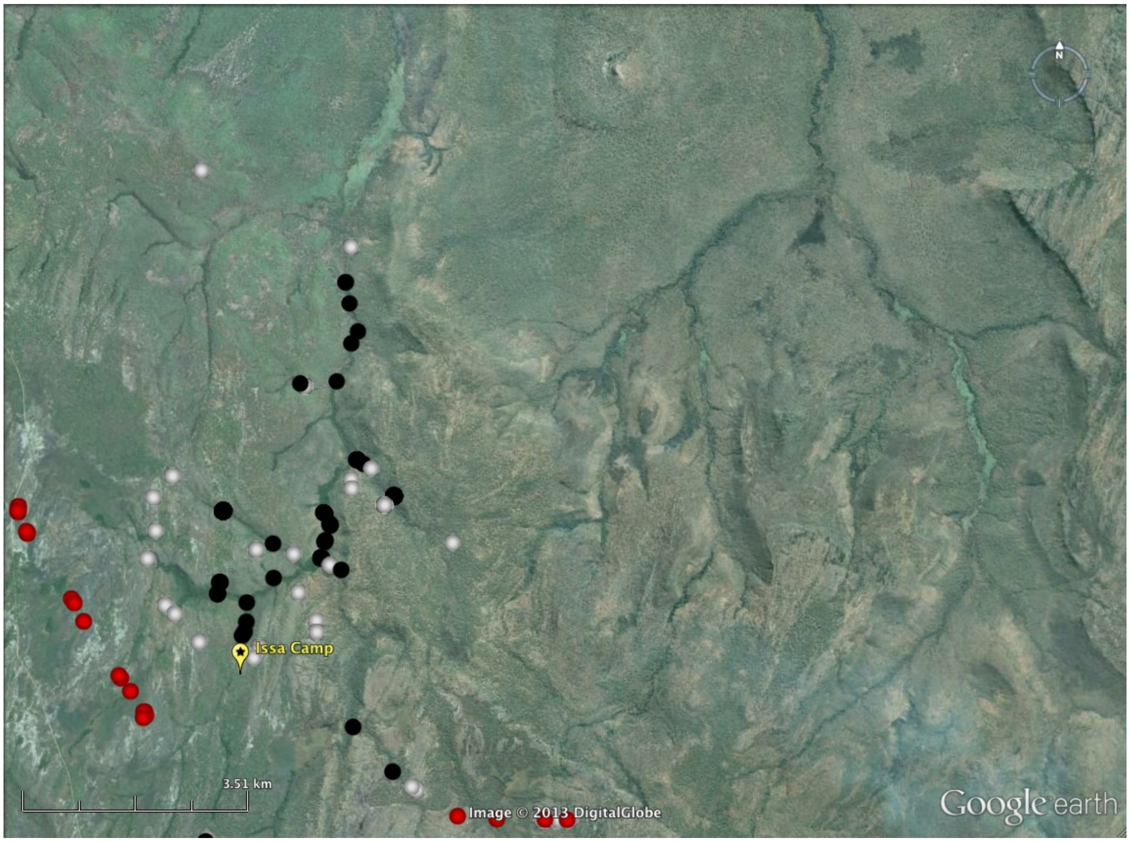


Figure 7-7. Distribution of all "other" encounters during this study. Red dots represent encounters in grassland/swamp, black dots represent encounters in forest, white dots represent encounters in woodland, and the yellow placemark represents camp.

Of the 6,418 total encounters, 3,271 (51%) occurred in woodland habitat, 2,887 (45%) occurred in forest habitat, and 260 (4%) occurred in grassland/swamp habitat. This distribution differs significantly from expectations relative to habitat availability (i.e., 90.5% woodland, 1.5% forest, 8% grassland/swamp), with fewer observations than expected in grassland/swamp and woodland habitats, and more observations than expected in forested areas ($\chi^2 = 82138.8$, df = 2, $p < 0.0001$). Figure 7-8 shows the number of encounters of Issa fauna occurring in patches, while Figure 7-9 gives the number of encounters of Issa fauna for each habitat type throughout the whole study area.

While the number of chimpanzee encounters were not included in the analyses here, these data are provided in both figures as a comparative reference.

In the previous chapter, results regarding chimpanzee habitat use were based on the analyses of four different subsets of data: patch focals only, all direct observations, all indirect observations, and all data (all direct and indirect observations combined). The results from the latter three data subsets did not differ significantly from one another, so analyses presented here are only for patch focals and all data sources combined; the analysis of the remaining two subsets would be repetitive and uninformative, so they are excluded here.

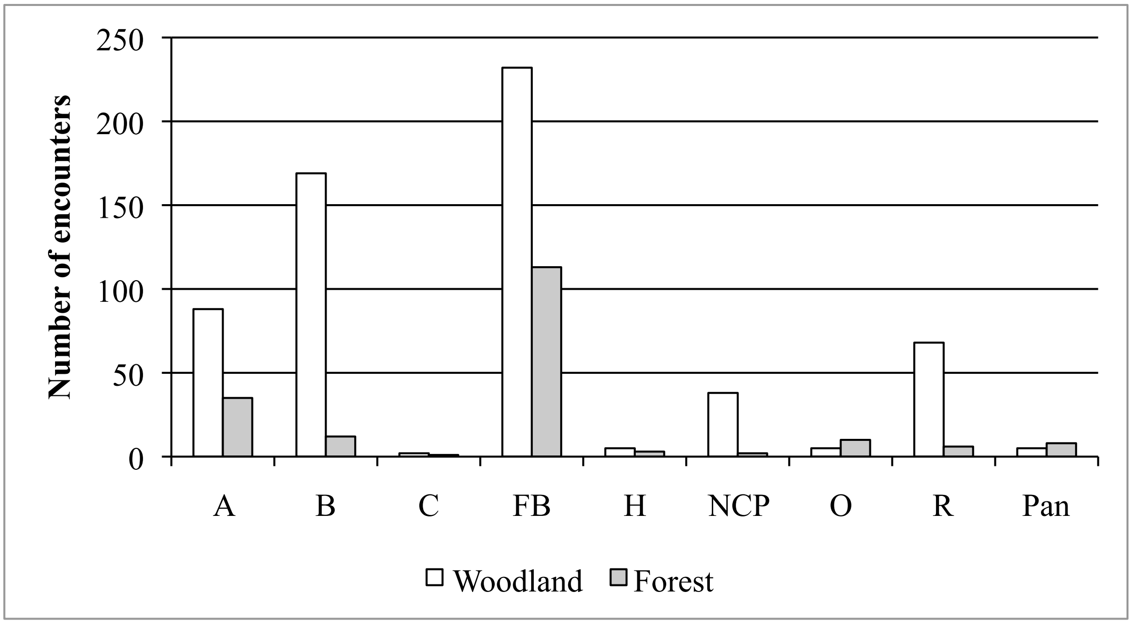


Figure 7-8. Number of encounters of Issa fauna in patches only. A: artiodactyls (n = 88 woodland, 35 forest, 121 total); B: non-frugivorous birds (n = 169 woodland, 12 forest, 181 total); C: carnivores (n = 2 woodland, 1 forest, 3 total); FB: frugivorous birds (n = 232 woodland, 113 forest, 345 total); H: herpestids (n = 5 woodland, 3 forest, 8 total); NCP: non-chimpanzee primates (n = 38 woodland, 2 forest, 40 total); O: others (n = 5 woodland, 10 forest, 15 total); R: rodents (n = 68 woodland, 6 forest, 74 total); Pan: chimpanzees (n = 5 woodland, 8 forest, 13 total).

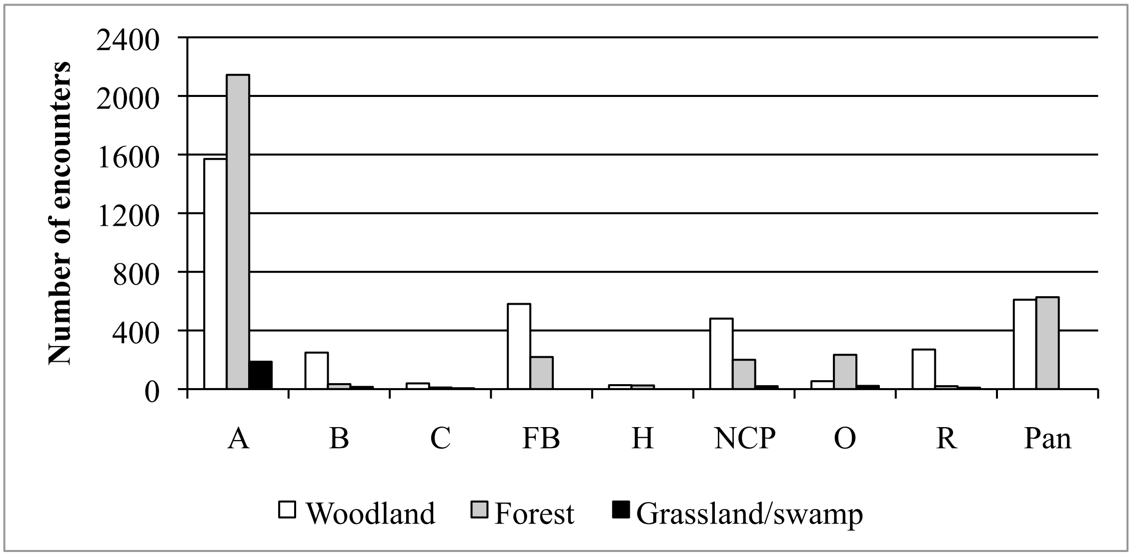


Figure 7-9. Number of encounters of Issa fauna in each habitat type throughout study site. A: artiodactyls (n = 1570 woodland, 2144 forest, 187 g/s, 3901 total); B: non-frugivorous birds (n = 249 woodland, 34 forest, 15 g/s, 298 total); C: carnivores (n = 39 woodland, 11 forest, 6 g/s, 56 total); FB: frugivorous birds (n = 581 woodland, 219 forest, 0 g/s, 800 total); H: herpestids (n = 27 woodland, 25 forest, 0 g/s, 52 total); NCP: non-chimpanzee primates (n = 481 woodland, 200 forest, 20 g/s, 701 total); O: others (n = 54 woodland, 234 forest, 22 g/s, 260 total); R: rodents (n = 270 woodland, 20 forest, 10 g/s, 300 total); Pan: chimpanzees (n = 610 woodland, 627 forest, 0 g/s, 1237 total).

While all faunal categories exhibited patterns of habitat use that significantly differed from those expected relative to habitat availability throughout the study area, use patterns varied between faunal categories. Figure 7-10 shows the breakdown of habitat use by each animal type.

Artiodactyls were encountered more often in forest than in woodland or grassland/swamp, at a much greater rate than expected ($\chi^2 = 75465.8$, df = 2, $p < 0.0001$). This pattern is not surprising as species that spent most of their time in forest (e.g., blue duikers) were encountered much more frequently than species that spent most, if not all, of their time in woodland (e.g., hartebeest, roan antelope). It is unclear, however, whether these differences in encounter rates were due to increased population densities of forest species, a bias in data sampling, or a combination of both factors. The extensive use of forest habitats by blue duikers, the preferred use of woodland habitats by the larger species, and the use of various habitat types by animals like bushpigs and bushbucks are all consistent with habitat use of these animals elsewhere (Estes, 1991; Bowland and Perrin, 1995; Kingdon, 1997; Skinner and Chimimba, 2005; Melletti et al., 2009).

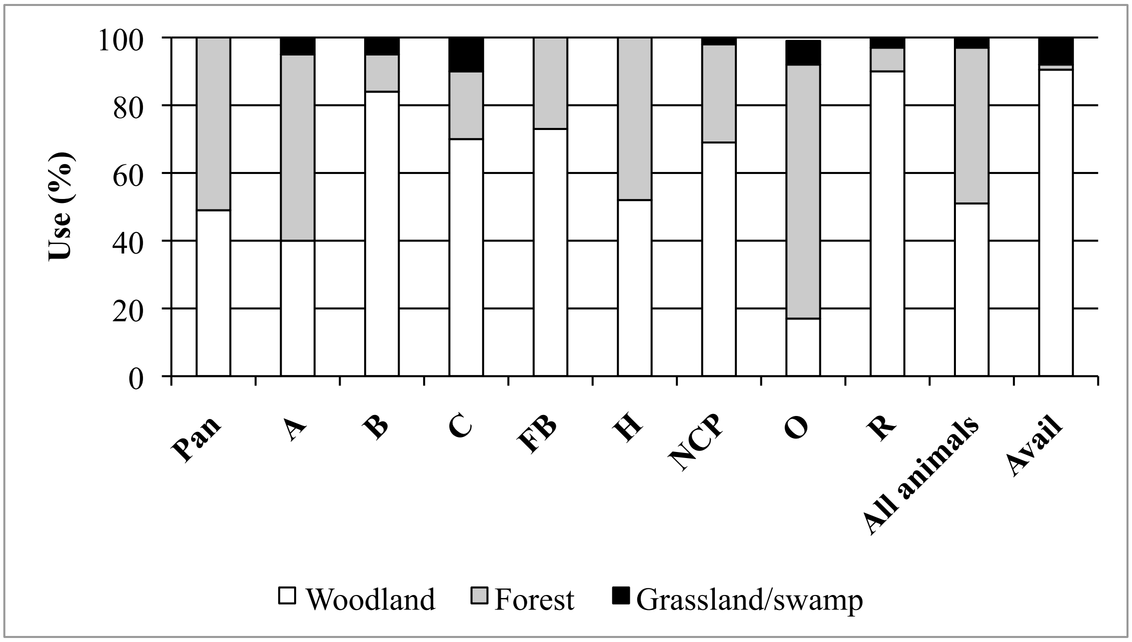


Figure 7-10. Percent use of each habitat type by all fauna throughout the study area. A: artiodactyls; B: non-frugivorous birds; C: carnivores; FB: frugivorous birds; H: herpestids; NCP: non-chimpanzee primates; O: others; R: rodents; Pan: chimpanzees; Avail: habitat availability.

Non-frugivorous birds used woodland habitats most often, followed by forest and then grassland/swamp. However, these animals were encountered in forest much more often than predicted by the limited availability of this habitat type ($\chi^2 = 199.95$, df = 2, p < 0.0001). Most encounters of non-frugivorous birds were of hawks or eagles flying over an area; these birds could potentially have an easier time finding prey in more open habitats as compared to closed forests, which would account for the greater use of woodland (Tanferna et al., 2013). Other terrestrial birds, like spurfowl and guineafowl, were almost always encountered foraging on the forest floors, which contributes to the greater than expected amount of forest encounters (Engills et al., 2009; Wiafe et al., 2010).

Carnivores showed the same overall pattern of habitat use as non-frugivorous birds, but used both forest and open grassland/swamp habitats much more than expected ($\chi^2 = 126.1$, df = 2, $p < 0.0001$). Leopards and hyenas were the two most frequently encountered carnivores during this study (leopards directly and hyenas indirectly), which might account for the habitat use patterns found for carnivores; leopards are found in a variety of habitats, but prefer those with dense vegetation (i.e., forest or closed woodland), while hyenas tend to prefer open grassland (Estes, 1991; Kingdon, 1997; Skinner and Chimimba, 2005; Pettorelli et al., 2009; Durant et al., 2010).

Frugivorous birds most often used woodland habitat, followed by forest, and were never encountered in grassland/swamp; this pattern of habitat use greatly differs from the availability of these habitats ($\chi^2 = 3663.0$, df = 2, $p < 0.0001$). It is understandable that frugivorous birds never used grassland/swamp areas, as these habitats have no trees for these birds to perch in or feed from. These results indicate that these birds are utilizing fruit from vegetative resources in both woodland and forest, which is not unlike the pattern found for chimpanzees. Turacos and hornbills at other East African sites seem to prefer more forested environments, but slight differences in habitat preferences between these birds at Issa and at other sites are likely correlated to differences in habitat availability (Whitney and Smith, 1998; Borghesio and Ndang'ang'a, 2003; Borghesio and Laiolo, 2004).

Herpestids appear to use both woodland and forest equally, but relative to habitat availability, they are using forest much more than expected and woodland much less than expected ($\chi^2 = 764.8$, df = 2, $p < 0.0001$). Most of the woodland encounters were of dwarf mongooses that use large termite mounds as dens and/or food sources, while bushy-tailed mongooses account for most of the forest encounters. Herpestids were never encountered in grassland/swamp, possibly because these habitats do not provide necessary cover for protection. These patterns of habitat use of Issa herpestids are consistent with those of herpestids at other sites (Waser et al., 1995; Caro and Stoner, 2003; Martinoli et al., 2006).

Primates, other than chimpanzees, were encountered most often in woodland environments, but still used forest much more than expected, and only very infrequently used grassland/swamp ($\chi^2 = 3474.9$, df = 2, $p < 0.0001$). Redtail, red colobus, and vervet monkeys were present at Issa, but found in low densities, so most of the non-chimpanzee primate encounters were with baboons. This bias in encounters of different species likely explains the large percentage of woodland use, as baboons used this habitat much more than forest. In contrast, redtail and red colobus monkeys were always encountered in forest, while vervet monkeys frequently used both woodland and forest habitats. Once again, these patterns of habitat use for each primate species are similar to those found at other sites (Cords, 1986; Barton et al., 1992; McGraw, 1994; Enstam and Isbell, 2002; Plumptre, 2006; Campbell et al., 2011; Iida et al., 2012).

Similar to artiodactyls, “other” animals were most frequently found in forest habitat, followed by woodland and grassland/swamp. This use of forest is much more than expected, while the use of grassland/swamp is what would be expected given the abundance of these habitat types ($\chi^2 = 11495.0$, df = 2, $p < 0.0001$). Most of the encounters in this category were of elephant shrews foraging in the leaf litter of forest floors, so it is not surprising that forest was the most used habitat. The use of extremely open grassland habitat is reflective of the encounters of hyraxes and hares, while other animals, such as genets and pangolins, were most often seen in forest, as would be expected based on their general habitat preferences at other sites (Estes, 1991; Kingdon, 1997; Skinner and Chimimba, 2005; Martinoli et al., 2006).

Rodents exhibited the greatest use of woodland and the least use of forest compared to all other animals, but still used habitats differently than expected based on their availabilities ($\chi^2 = 61.56$, df = 2, $p < 0.0001$). This category consists mostly of encounters of squirrels and porcupines, animals that more often use woodland habitats as compared to forest (Emmons, 1980; Estes, 1991; de Villiers and Aarde, 1994; Corbet and Aarde, 1996; Kingdon, 1997).

The general patterns of habitat use relative to habitat availability for each animal category persist throughout the whole year, regardless of seasonality. However, when examining use within each habitat type, seasonal patterns of habitat use exist for most animals. Table 7-1 summarizes these patterns and provides chi-squared values for each animal category.

Overall, animals used both woodland and forest habitats more in the dry season than in the wet season. Artiodactyls, all birds, and non-chimpanzee primates exhibited this pattern. However, this pattern most likely does not have any ecological significance, but simply reflects an increased number of animal encounters during the dry season as compared to the wet season. During the dry season, natural and man-made fires burn all of the woodland grasses making it easier to directly observe animals and find signs (e.g., scat, prints, etc.).

Table 7-1

Summary of seasonal habitat use patterns within each habitat type (not relative to habitat availability; all chi-square analyses had df=1, bolded values indicate significance)

	Woodland	**chi-square values**	**Forest**	**chi-square values**	**Grassland/ swamp**	**chi-square values**
Artiodactyls	**> dry**	**$\chi^2 = 127.8$, $p < 0.0001$**	**> dry**	**$\chi^2 = 50.8$, $p < 0.0001$**	no difference	$\chi^2 = 1.2$, $p = 0.27$
Birds	**> dry**	**$\chi^2 = 14.9$, $p = 0.0001$**	**> dry**	**$\chi^2 = 5.8$, $p = 0.02$**	no difference	$\chi^2 = 0.6$, $p = 0.44$
Carnivores	**> dry**	**$\chi^2 = 5.16$, $p = 0.023$**	no difference	$\chi^2 = 2.27$, $p = 0.13$	**> dry**	**$\chi^2 = 6.0$, $p = 0.014$**
Frugivorous Birds	**> dry**	**$\chi^2 = 25.2$, $p < 0.0001$**	**> dry**	**$\chi^2 = 56.26$, $p < 0.0001$**	N/A	
Herpestids	no difference	$\chi^2 = 0.04$, $p = 0.85$	no difference	$\chi^2 = 0.36$, $p = 0.55$	N/A	
Non-Chimpanzee Primates	**> dry**	**$\chi^2 = 27.49$, $p < 0.0001$**	**> dry**	**$\chi^2 = 59.11$, $p < 0.0001$**	no difference	$\chi^2 = 1.8$, $p = 0.18$
Others	no difference	$\chi^2 = 1.19$, $p = 0.28$	**> dry**	**$\chi^2 = 17.5$, $p < 0.0001$**	no difference	$\chi^2 = 1.64$, $p = 0.2$
Rodents	**> dry**	**$\chi^2 = 35.6$, $p < 0.0001$**	no difference	$\chi^2 = 0.2$, $p = 0.65$	**> dry**	**$\chi^2 = 6.4$, $p = 0.011$**
All non-chimpanzee fauna	**> dry**	**$\chi^2 = 219.9$, $p < 0.0001$**	**> dry**	**$\chi^2 = 140.9$, $p < 0.0001$**	no difference	$\chi^2 = 0.75$, $p = 0.39$

BEHAVIOR ACROSS HABITAT TYPES

When any animal was encountered during this study, its behavior was recorded as travel, rest, or eat. However, most encounters of fauna outside of patch focals consisted of the individual running away from the observer. Therefore, data presented here are from patch focals only. Furthermore, for each animal group, the activity budget did not change with season, so all analyses here are for the entire study period.

A total of 789 encounters of non-chimpanzee fauna were recorded during patch focals. Animals were traveling during 73% of these encounters, resting in 23%, and eating in 4%. In general, traveling and resting occurred more often in woodland than forest, while eating was observed almost equally in both habitat types. However, behavioral patterns across habitat types differed among faunal categories (Figure 7-11).

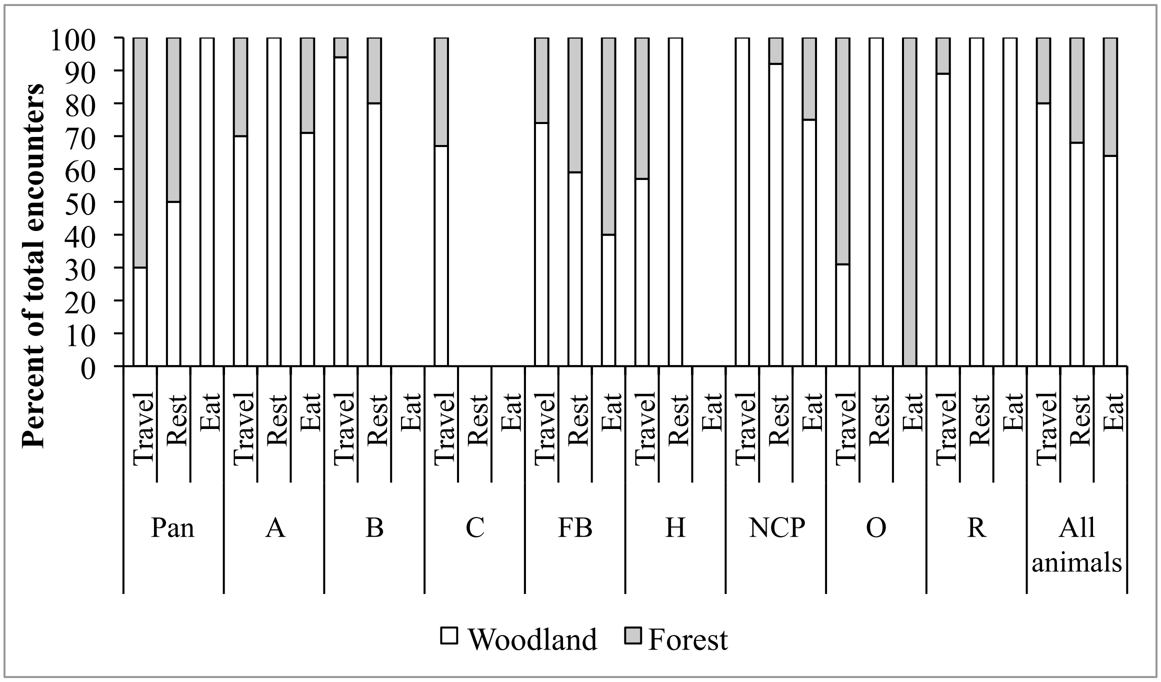


Figure 7-11. Behavior of Issa fauna in patches, based on encounters.

For artiodactyls, non-chimpanzee primates, and rodents all behaviors occurred more in woodland than in forest. Similarly, more encounters of animals resting and travelling in woodland occurred for non-frugivorous birds and herpestids, but these animals were never encountered while eating. Carnivores were only ever encountered travelling, and did so more in woodland than in forest. Frugivorous birds were observed eating more in forest as compared to woodland, but travelled and rested more in woodland habitats. Other animals also rested more in woodland habitats, but were observed travelling and resting more in forest.

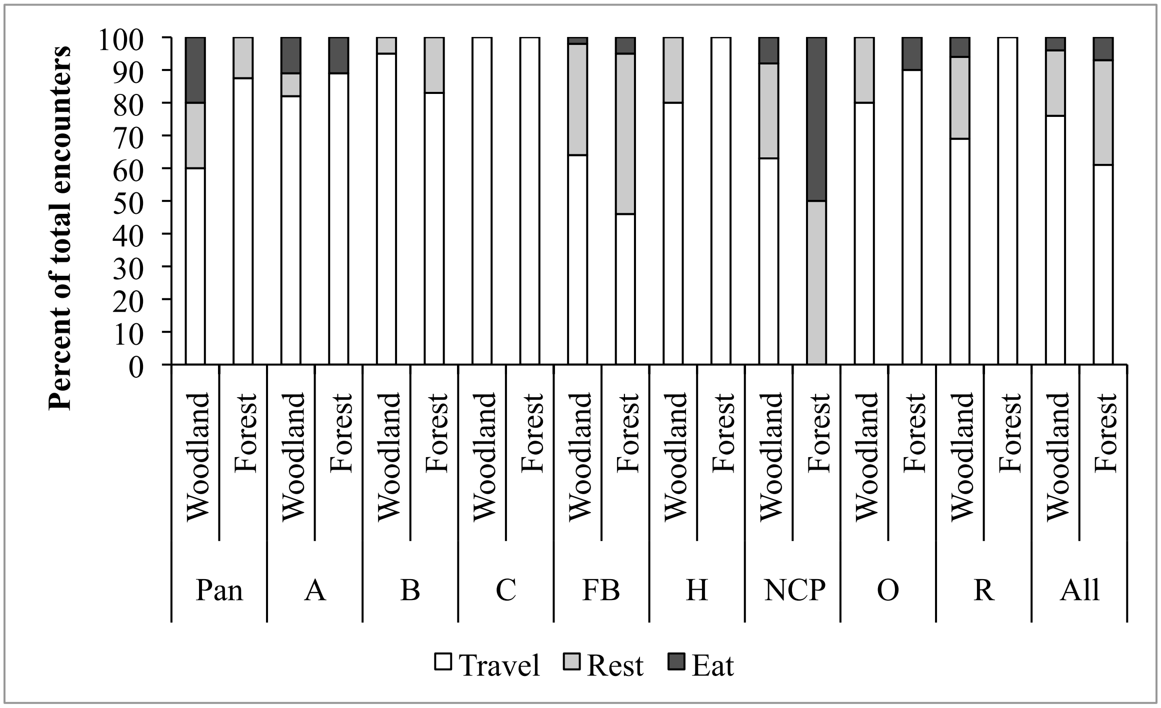


Figure 7-12. Behavior of Issa fauna in patches within habitat types, based on encounters.

Examining behavioral patterns within habitat types, shows that most animals were encountered travelling as compared to resting or eating in both woodland and forest habitats. However, these patterns differed across faunal categories (Figure 7-12). All animal species exhibited the same behavioral pattern when in woodland; animals were mostly encountered travelling, followed by resting, and then eating. Artiodactyls, non-frugivorous birds, carnivores, and herpestids showed the same activity pattern when encountered in forest. In contrast, when in the forest frugivorous birds were observed to be resting most frequently, followed by travelling and then eating. Non-chimpanzee primates in forest were observed to rest and eat an equal number of times, with both behaviors occurring more than travel.

In general, most patch focal encounters of non-chimpanzee fauna consisted of them travelling within or through the patch. Observations of eating and resting varied by animal species both across and within habitat types.

USE OF DIETARY (FOOD) RESOURCES

During this study only a limited number of direct feeding observations were made in which the plant item eaten could be identified to genus or species level. These observations consisted of turacos eating two fruit species also eaten by chimpanzees (*Ficus exasperata* and *Saba comorensis*), baboons eating six fruit species also eaten by chimpanzees (*Diplorhynchus condylocarpon*, *Ximenia caffra*, *Vitex doniana*, *Brachystegia spiciformis*, *B. utilis*, and *B. bussei*), and squirrels eating three fruit species also eaten by chimpanzees (*Brachystegia bussei*, *B. spiciformis*, and *Ximenia caffra*). Due to the small sample size of these observations, all analyses presented here were performed on data from fecal samples only, and not from direct observations.

A total of 227 fecal samples of mammals other than chimpanzees were collected throughout the study period and analyzed for content. Artiodactyl fecals included those from blue duiker (n = 17), buffalo (n = 1), bush duiker (n = 5), bushbuck (n = 13), bushpig (n = 12), eland (n = 3), reedbuck (n = 1), hartebeest (n = 5), klipspringer (n = 6), and roan antelope (n = 13). The carnivore samples consisted of two leopard fecals and two hyena fecals. Non-chimpanzee primate samples included 109 baboon fecals, 1 red colobus fecal, and 18 redtail monkey fecals. All of the rodent fecals came from porcupines. No fecal samples were obtained for birds or herpestids.

Of the 76 artiodactyl fecal samples, most were from animals that are classified as grazers and/or browsers, so it is not unexpected that most fecal samples contained only chewed vegetation and/or fibrous vegetative material. Only two samples contained any fruit seeds; one sample from a blue duiker (containing *Ficus* seeds) and one sample from a bushpig (Table 7-2). There was an expectation of finding more fruit seeds contained in fecal samples from blue duikers, bushpigs, and bushbuck, as these animals have been observed to eat fruit elsewhere (Dubost, 1984; Estes, 1991; Faurie and Perrin, 1993; Fa and Purvis, 1997; Kingdon, 1997; Skinner and Chimimba, 2005). In a study of diet of extant African bovidae, Gagnon and Chew (2000) found that frugivorous diets were attributed exclusively to duikers (*Cephalophus* sp.) as compared to other bovids.

Carnivore samples contained copious amounts of animal hair and bone, all expected items (Figure 7-13). "Other" samples consisted of one otter fecal containing over 90% crab shell, and two aardvark fecals containing a mixture of ants and termites. The presence and amounts of these food items are consistent with what is known about otter and aardvark diets (Estes, 1991; Kingdon, 1997).

Of the 17 porcupine fecal samples, three contained at least one species of fruit seed (Table 7-2); one of the two plant species represented is also part of the chimpanzee diet. Chewed roots were found in 76% of fecal samples and invertebrates (ants and termites) were found in 24% of samples. This is consistent with what is known for porcupine diets elsewhere, in that they eat a variety of fruits, leaves, roots, bulbs, invertebrates, and bark (Estes, 1991; Kingdon, 1997; Barthelmess, 2006).

Table 7-2
Plant species consumed by bushpig and porcupines, from fecal analysis

	Family	**Species**	**Habitat**
Bushpig	Apocynaceae	*Saba comorensis*	Forest
	Myrtaceae	*Syzygium guineense*	Woodland
Porcupine	Anacardiaceae	*Sclerocarya birrea*	Woodland
	Fabaceae	*Brachysegia spiciformis*	Woodland

Figure 7-13. Items found in two hyena fecal samples.

Of 18 total redtail monkey fecal samples, 15 (83%) contained at least one kind of fruit seed, representing a total of eight different plant species (Table 7-3). Additionally, fig seeds (*Ficus* sp.) were found in six (33%) samples, termites were found in 11% of samples, and 22% of fecal samples contained chewed vegetation. This dietary profile of Issa redtail monkeys is similar to that of redtail monkeys at other sites across East Africa (Cords, 1986; Fa and Purvis, 1997; Chapman et al., 2002; Campbell et al., 2011; Bryer et al., 2013).

Table 7-3
Plant species consumed by redtail monkeys, from fecal analysis

Family	**Species**	**Habitat**
Annonaceae	*Uvaria* sp.	Forest
Loganiaceae	*Strychnos cocculoides*	Forest
Loganiaceae	*Strychnos* sp.	Forest/Woodland
Rubiaceae	*Rothmannia* sp.	Forest
Rutaceae	*Toddalia asiatica*	Forest
Tiliaceae	*Grewia rugosifolia*	Woodland
Vitaceae	*Ampelocissus obtusata*	Forest
Zingiberaceae	*Aframomum mala*	Forest/Woodland/Wooded Grassland

A total of 109 baboon fecal samples were analyzed for content. Of these, 55% contained at least one type of fruit seed, 9% contained seeds from *Ficus* sp., 53% contained invertebrates, 40% contained chewed vegetation, and 47% had chewed roots. A total of 23 different plant species were represented in these fecal samples; 16 of these were positively identified to genus and/or species level (Table 7-4). All of these identified species are also known to be a part of the chimpanzee diet, while two of the unidentified species were only found in baboon fecals, and not in chimpanzee fecals. The broad and varied diet of Issa yellow baboons is similar to the diet of yellow baboons at other study sites, which consist of a mixture of fruit, seeds, leaves, flowers, grasses, herbs, and animal matter (Post, 1982; Norton et al., 1987; Whiten et al., 1991b; Campbell et al., 2011).

Table 7-4
Plant species consumed by baboons, from fecal analysis

Family	**Species**	**Habitat**
Annonaceae	*Annona senegalensis*	Woodland
Annonaceae	*Monanthotaxis poggei*	Forest
Apocynaceae	*Saba comorensis*	Forest
Clusiaceae	*Garcinia huillensis*	Forest/Woodland
Dioscoreaceae	*Tacca loentopetaloides*	Woodland
Fabaceae	*Brachysegia spiciformis*	Woodland
Flacourtiaceae	*Flacourtia indica*	Forest
Loganiaceae	*Strychnos cocculoides*	Forest
Loganiaceae	*Strychnos* sp.	Forest/Woodland
Phyllanthaceae	*Uapaca kirkiana*	Woodland
Phyllanthaceae	*Uapaca nitida*	Woodland
Rubiaceae	*Rothmannia* sp.	Forest
Sapindaceae	*Zanha africana*	Woodland
Tiliaceae	*Grewia rugosifolia*	Woodland
Verbenaceae	*Vitex doniana*	Woodland
Zingiberaceae	*Aframomum mala*	Forest/Woodland/Wooded Grassland

INTERSPECIFIC INTERACTIONS

As discussed in Chapter 2, interactions between species are an important part of the ecology of a faunal community. These interactions can be neutral for both species, beneficial to both species (i.e., mutualism), beneficial to only one species (i.e., predation), or negative for both species (i.e., competition).

NEUTRALISM

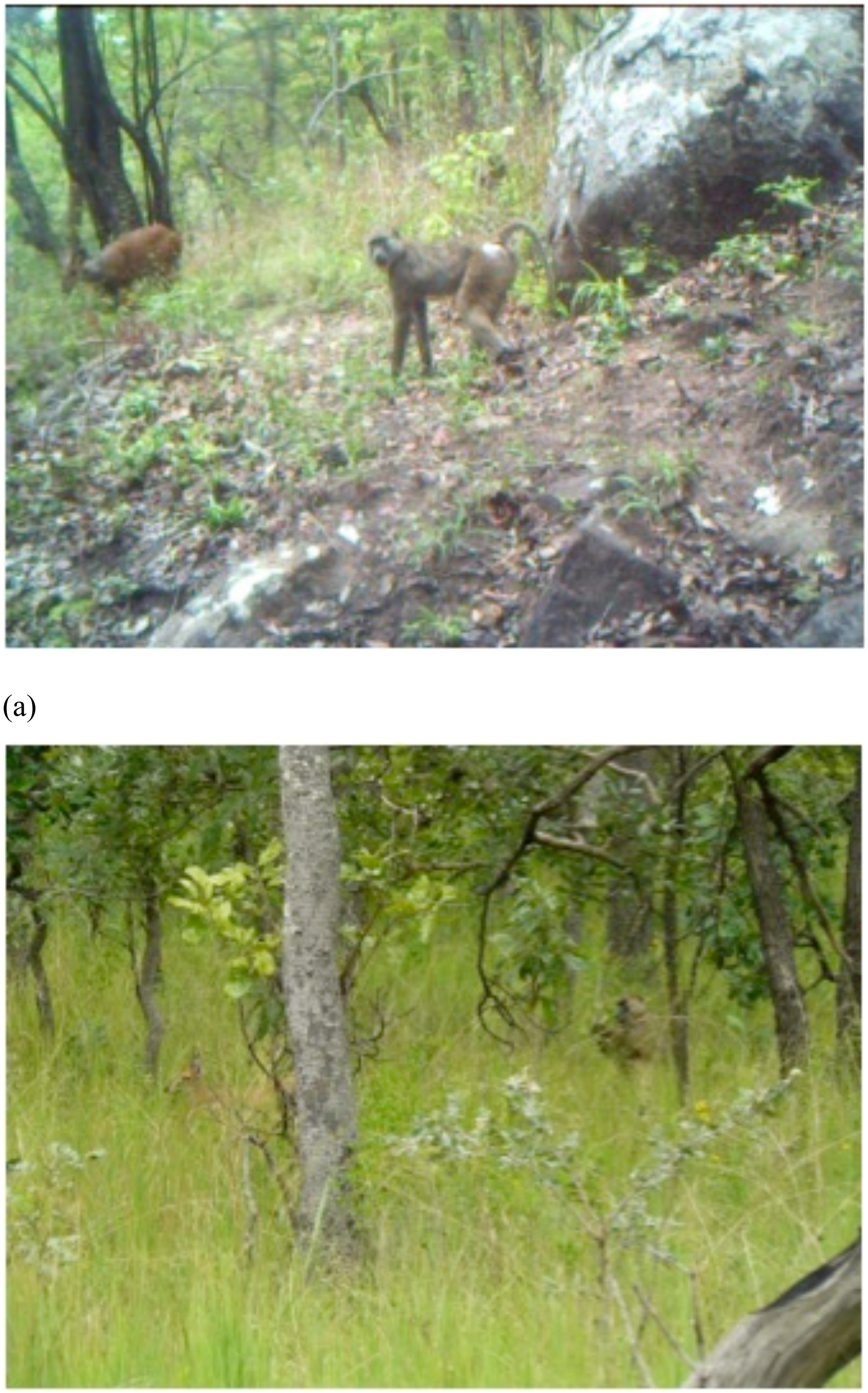
Neutral interspecific interactions are often observed when two or more species are in spatial proximity to one another and are simply tolerating each other's presence without exhibiting any positive (e.g., cooperation, play, etc.) or negative (e.g., threats, displays, etc.) behaviors toward the other species (Tokeshi, 1999). Only a few instances of neutralism were observed during this study, most often involving the presence of an artiodactyl (e.g., bushbuck, blue duiker, bush duiker) and one or more individuals of another species. Blue duikers were often seen foraging in the same space as elephant shrews, while both bushbuck and bush duikers were observed to share space with baboons on multiple occasions (Figure 7-14). A small group of vervet monkeys were also observed in close proximity to a blue duiker on one occasion, but the vervets stayed up in the trees during the entire shared encounter. On another occasion, a small group of redtail monkeys were observed to share space with an adult female bushbuck. Once again, the monkeys remained in the trees for the entire encounter, but did not seem stressed or more vigilant due to the bushbuck's presence. The only other neutralistic interspecific interaction during this study occurred when a bush squirrel and a family of dwarf mongooses were all foraging around the same termite mound. Issa chimpanzees were never observed to directly share space with another species at the same time.

MUTUALISM/COOPERATION

During this study no mutualistic or cooperative associations were observed. However, there is a potential for polyspecific associations between bovid species, since numerous species use the same habitat types and eat similar foods at Issa. Polyspecific associations between primates are less likely at Issa, as there is only one guenon species (i.e., redtail monkeys), and other primates such as baboons and vervets are not known to form such mixed-species associations.

PREDATION

Directly observing instances of predation are extremely rare, so it was not unexpected that predation was never directly observed during this study. However, in addition to the carnivore fecal samples mentioned above, encounters of carcasses and bones indicate the presence of predators at Issa. On one occasion, an eagle was encountered preying upon the carcass of a blue duiker, but it is unclear whether the eagle had killed the duiker or had scavenged it. Bones of other animals (e.g., bovids, baboons, snakes) were also found throughout the study area during this study, but the death of these animals could not positively be attributed to predation, as compared to illness or hunting as cause of death.



(a)

(b)

Figure 7-14. Neutralistic interaction between a baboon and bushbuck (a) and a baboon and bush duiker (b).

COMPETITION

Competition over spatial and dietary resources can occur both directly and indirectly. Direct, or interference competition, was only ever observed between members of the same species (i.e., intraspecifically) during this study. Indirect, or exploitative, competition is more difficult to observe, as it involves the depletion of resources by one species while the other species is not present. Therefore, measures of resource overlap have often been used as proxies for levels of indirect competition (Pontin, 1982; Arthur, 1987; Tokeshi, 1999; Keddy, 2001).

Competition for spatial resources

As discussed in the previous chapter, chimpanzees used forest habitat much more than expected relative to its availability. When habitat availability is overlooked, chimpanzees appear to use both woodland and forest habitat equally. Other animals at Issa also exhibited a greater use of forest relative to its availability, but vary in habitat selectivity when availability is overlooked. Artiodactyls and "other" animals are more prevalent in forest, while birds, carnivores, rodents, and non-chimpanzee primates appear to use woodland habitats more often than forest. Therefore, all of these animals are potential competitors for each other in terms of spatial resources. In order to quantify the degree to which species overlap in spatial resource use, Czekanowki's index was calculated. Only data from patch focals were used in these analyses due to the inconsistent nature of data collection at other times.

Czekanowki's index provides an assessment of the symmetrical overlap of resource use between two species (Krebs, 1999). The formula is:

$$O_{12} = O_{21} = 1 - \tfrac{1}{2} \Sigma \left| p_{1j} - p_{2j} \right|$$

where O is the overlap of species 1 and 2, and p_{1j} is the proportion of all encounters of species 1 in patch j. Table 7-5 lists the index values of each animal category compared to chimpanzees. Both herpestids and carnivores have an index value of 0, indicating that they are not competing at all with chimpanzees for spatial resources in patches. This result is likely underestimated due to small sample sizes of herpestid and carnivore encounters, but if competition between these groups did exist, it would be minimal. Non-frugivorous birds and non-chimpanzee primates both had about a 10% in spatial resources with chimpanzees, indicating very minimal competition. Rodents and artiodactyls had a slightly higher overlap percentage, but still fell below 20% overlap, meaning very little competition between these groups and chimpanzees for spatial resources. Frugivorous birds shared about 23% of spatial resources with chimpanzees, which points to some, but not much, competition between these groups. Finally, “other” animals showed the greatest overlap with chimpanzees (57%), implying a large amount of competition between these two groups. However, this category consists of many different kinds of animals (e.g., pangolins, hyraxes, macroscelids, genets, etc.), so it is likely that each of these species individually is not a common competitor of spatial resources with chimpanzees. Grouping all of the non-chimpanzee fauna together provides an assessment of community-wide competition for spatial resources. Chimpanzees and other fauna overlap in patch habitat use by 18%, again indicating minimal competition between these species for spatial resources.

Table 7-5
Overlap of spatial resources between animal categories and chimpanzees

	Czekanowski Index	**Percent overlap**
Artiodactyls	0.161	16.1%
Non-frugivorous birds	0.099	9.9%
Carnivores	0.000	0.0%
Frugivorous Birds	0.227	22.7%
Herpestids	0.000	0.0%
Non-Chimpanzee Primates	0.100	10.0%
Others	0.574	57.4%
Rodents	0.185	18.5%
All non-chimpanzee fauna	0.183	18.3%

Competition for dietary resources

Similar to chimpanzees at other sites, the diet of Issa chimpanzees consists mostly of fruit and leaves. Since fruits are fewer in abundance throughout the year as compared to leaves, the focus here on dietary competition between chimpanzees and other animals is on the overlap in the number of fruit resources used. Most artiodactyls at Issa are browsers and/or grazers, but blue duikers and bushpigs do eat a minimal amount of fruit. The diet of rodents, particularly squirrels and porcupines, also contain a number of fruits that are found in the chimpanzee diet. Frugivorous birds were observed numerous times eating fruits of plant species that chimpanzees also eat. Unfortunately, no avian fecal samples were analyzed in this study. Lastly, fruit is a major component of the diets of non-chimpanzee primates, particularly redtail monkeys and baboons. In order to quantify the degree of dietary overlap between chimpanzees and other animals, Pianka's index was calculated based only on the information obtained from fecal samples.

Pianka's index provides an assessment of the amount of overlap in the diet of two species (Krebs, 1999). The formula is:

$$O_{jk} = \Sigma\ p_{ij}p_{ik}/(\Sigma p_{ij}^{2}\Sigma p_{ik}^{2})^{1/2}$$

where O is the overlap of species j and k, and p_{ij} is the proportion of food item i in the diet of species j and k. Table 7-6 lists the index values for dietary overlap between chimpanzees and other frugivorous fauna for which there were fecal samples. Bushpigs showed the least amount of overlap, followed by porcupines. While these animals do eat some of the same food items as chimpanzees, the degree of dietary overlap is minimal, indicating a very small amount of competition. Furthermore, any fruits eaten by bushpigs and porcupines are those found on the ground as opposed to in the trees, providing another way to lessen competition between these animals and chimpanzees. Of the two non-chimpanzee primate species evaluated, redtail monkeys had three times as much overlap with chimpanzees as compared to baboons. This reflects a greater reliance on fruits by redtails relative to baboons, and the broader diet consumed by baboons. Even so, the amount of competition between redtails and chimpanzees for fruit is not large (36%). While this overlap percentage is not small, differences in foraging habits between these primates will minimize potential competition for resources. Redtails spend the majority of their time in forest, so almost all of the fruit in their diet comes from forest trees or woodland trees on the edge of the forest. In contrast, chimpanzees spend their time in both woodland and forest, and regularly consume fruit from both woodland and forest trees. Additionally, these results are most likely overestimating the amount of overlap in resource use, because the consumption of different parts of the same plant species is not accounted for.

Table 7-6
Overlap of dietary resources between frugivorous species and chimpanzees, based on fecal analysis

	Pianka Index	**Percent Overlap**
Bushpigs	0.057	5.6%
Porcupines	0.095	9.5%
Redtail monkeys	0.362	36.2%
Baboons	0.118	11.8%

DISCUSSION

Overall, the resource use patterns of non-chimpanzee fauna at Issa are similar to patterns of resource use by these animals at other sites. While chimpanzees share spatial and dietary resources with many of these species, there is only minimal overlap in the use of habitat space and food items. Therefore, it appears that chimpanzees have very little competition for space or food at Issa. Furthermore, this competition is not coming from other primates as is usually assumed, but more likely from other frugivorous animals including birds, squirrels, and bats (though bats were not considered in this study). Unfortunately the degree to which the diets of these species overlap with chimpanzee diet could not be determined during this study, as no fecal samples were obtained from these species.

These results emphasize the need to study communities in terms of dietary or spatial guilds (e.g., frugivory) as compared to phylogeny (e.g., primates). Other studies have focused on the relationships between primates, birds, bats, squirrels, and ruminants (Emmons, 1980; Gautier-Hion et al., 1980; Emmons et al., 1983; Poulsen et al., 2003; Garber and Sussman, 2005; Marshall et al., 2009), but no study has yet looked at this aspect of community ecology for great apes, other than orangutans (Beaudrot et al., 2013). However, some information about the relationships between frugivorous fauna at other chimpanzee sites can be pieced together from multiple research projects. The next chapter discusses the similarities and differences of the faunal community at Issa to fauna at other chimpanzee sites.

CHAPTER 8: OTHER CHIMPANZEE COMMUNITIES

Comparing the community ecology of Issa with that of other chimpanzee sites can further elucidate the ecological role occupied by Issa chimpanzees. The availability and utilization of both spatial and dietary resources has been well researched at other sites for chimpanzees, and for other primates to a somewhat lesser extent. In contrast, non-primate species have largely been ignored. Until now, only one other chimpanzee study has discussed the presence of, and possible competition for chimpanzee resources by, non-primate frugivores (Ghiglieri, 1984); this study, however, only focused on a limited number of food items and relied solely upon opportunistic feeding observations of non-chimpanzee fauna.

Therefore, due to differences in research questions and methods, direct quantitative comparisons cannot be made between the research presented in this dissertation and that of other chimpanzee studies. Nonetheless, examining the results of multiple studies across sites can reveal general similarities and differences between Issa chimpanzees and other communities.

Ecological aspects of the Issa community are compared to those of well-established chimpanzee sites that can be classified into one of three categories, loosely based on the amount of annual rainfall received: "wet", "intermediate", or "dry" sites, with the latter receiving less than 1500mm of annual rainfall and/or having $\geq$ 5 dry months, i.e., months with less than 100mm rain (Table 8-1). "Wet" sites include Tai located in Cote d'Ivoire, and the sites of Budongo and Kibale both located in Uganda; "intermediate" sites include Gombe and Mahale, both located in western Tanzania; and "dry" sites include Assirik and Fongoli both in Senegal, as well as Semliki located in Uganda. While other brief studies and surveys of dry-habitat chimpanzees in Eastern Africa exist (e.g., Izawa and Itani, 1966; Suzuki, 1969; Izawa, 1970; Moore, 1992), Semliki and Issa are the only two well-established, ongoing research sites.

RAINFALL AND SEASONALITY

By definition, the wetter sites of Tai, Kibale, and Budongo have the highest average annual rainfall and the shortest dry seasons (Table 8-1). In contrast, the dry sites of Assirik and Fongoli receive the least amount of rain annually and have the longest dry seasons. The other dry site, Semliki, has a slightly greater amount of annual rainfall and a less lengthy dry season compared to other dry sites.

The amount of annual rainfall at Issa falls within the range of dry sites, but more closely resembles Semliki as compared to the two Senegalese sites. The length of dry season at Issa is most similar to those of the intermediate sites of Gombe and Mahale, while average daily temperatures at Issa most closely resemble those of other dry sites. The range in mean daily temperatures appear to be the most extreme at Issa compared to all other sites, but this result might be the outcome of the different methods used across sites (e.g., Issa temperatures are reflective of measurements from multiple locations in all habitat types, while other sites might report temperature from a single location and/or habitat type only).

Table 8-1

Rainfall, seasonality, and temperature range of select chimpanzee study sites; shaded rows are dry sites

Site	**Mean Annual Rainfall (mm)**	**Length of Dry Season**	**Mean Daily Temperature**
Tai[1]	1829	3 months	24-28°C
Kibale[2]	1671-1800	4 months	16-23°C
Budongo[3]	1684-1842	3 months	14-28°C
Gombe[4]	1600-1775	4-5 months	19-28°C
Mahale[5]	1774-1836	4-5 months	18-30°C
Assirik[6]	954	7 months	23-35°C
Fongoli[7]	900-1100	8 months	25-33°C
Semliki[8]	1450	4 months	19-34°C
Issa[9]	955-1537	5-6 months	14-36°C

[1] Boesch and Boesch-Achermann, 2000; Lehman and Boesch, 2003; [2] Wrangham et al., 1996; Struhsaker, 1997; [3] Newton-Fisher, 1999; Reynolds, 2005; [4] Goodall, 1986; Wallis, 1997; [5] Nishida, 1990; Nishida et al., 2003; [6] McGrew et al., 1981; Hunt and McGrew, 2002; [7] Pruetz, 2006; [8] Hunt and McGrew, 2002; [9] this study; Hernandez-Aguilar, 2006; Stewart, 2011

DEMOGRAPHICS

In general, chimpanzee populations at all sites compared here are of similar sizes, with Assirik having the smallest population size of 28 individuals (Table 8-2). Likewise, most sites have an average party size of 4-6 individuals, with Tai having the largest average parties made up of eight individuals. Chimpanzee densities vary greatly across wet and intermediate sites; discrepancies in densities within and between sites are likely a result of the use of different methods (e.g., nest counts versus direct counts; Hashimoto, 1995; Marchesi et al., 1995; Plumptre and Reynolds, 1996; Plumptre and Reynolds, 1997). Despite problems with measuring density, it is clear that chimpanzees at all dry sites occur at lower densities as compared to wet sites.

The chimpanzees at Issa have an estimate average population size of 72 individuals, a much larger number of individuals than chimpanzees counted at the other dry sites of Assirik and Fongoli. While chimpanzee population size at Issa was determined based on the presence of DNA from hairs found in nests, population sizes at Assirik and Fongoli were determined based on observations of individual (unhabituated) chimpanzees. Therefore, it is possible that chimpanzee population size is underestimated at these latter two sites. When considering average party size, however, Issa's parties are smaller than at all other sites. There are two reasons that could explain this phenomenon: 1) Issa chimpanzee party demography could potentially exist as a way to reduce intraspecific feeding competition, or 2) party size is underestimated due to the lack of chimpanzee habituation. Thus, as food resources at Issa are not limited, the number of average party size is more likely due to the latter explanation. Density of Issa chimpanzees, based on nest counts, matches the densities calculated for all other dry sites, which also associates with Issa chimpanzees having a much larger home range than chimpanzees at intermediate or wet sites.

Table 8-2

Demographics of select chimpanzee study sites; shaded rows are dry sites

Site	Population Size	Average Party Size	Density
Tai[1]	29-82	8.3	0.69-1.7/km^2
Kibale (Kanyawara)[2]	45-50	5.1	2.75/km^2
Budongo[3]	32-62	5.7	2.12-2.22/km^2
Gombe[4]	38-60	4.5	1.46-5/km^2
Mahale[5]	45-101	6.1	0.96-4.3/km^2
Assirik[6,7]	28	4.0	0.09-0.13/km^2
Fongoli[7]	36	4.1	0.09/km^2
Semliki[8]	104	4.8	not reported
Issa[9]	72	3.0	0.08-0.12/km^2

[1]Kouakou et al., 2009; [2]Chapman and Wrangham, 1993; [3]Plumptre et al., 2003; [4]Wrangham, 1977; Baldwin et al., 1982; Goodall, 1986; [5]Nishida et al., 1990; [6]Baldwin et al., 1981; [7]Pruetz et al., 2002; [8]Samson, 2012; [9]Kano, 1972; Ogawa et al., 2007

HABITAT AVAILABILITY AND USE

General habitat descriptions of the comparative set of chimpanzee study sites are given in Table 8-3; the distribution of each habitat type is also given, if the information was available in the published literature. It is clear that forests are an important habitat for chimpanzees, as this habitat type is present at all study sites. While the presence of forested areas is necessary for chimpanzee survival, the forest area does not need to be abundant; at all dry sites, gallery forest accounts for 3% or less of all available habitat types. Another difference at Issa involves woodland versus grassland as compared with both Assirik (55%) and Fongoli (36%) having much more grassland than Issa (8%), and considerably less woodland area.

Table 8-3
Habitat descriptions and availability for select chimpanzee study sites; shaded rows are dry sites

Site	Habitat	Reference
Tai	Moist evergreen forest	Boesch and Boesch-Achermann, 2000
Kibale	evergreen forest, forest-grassland, swamp (3%)	Struhsaker, 1997; McGrew et al., 1996
Budongo	semi-deciduous tropical rain forest	Reynolds, 2005;
Gombe	evergreen riverine forest, deciduous dry forest, thicket, grassland, moorland	Collins and McGrew, 1988
Mahale	tropical semi-evergreen forest, miombo woodland	McGrew et al., 1996
Assirik	gallery forest (3%), woodland (37%), bamboo thicket (5%), grassland (55%)	McGrew et al., 1981
Fongoli	gallery forest (2%), woodland (46%), bamboo (12%), cultivated field (4%) grassland (36%)	Pruetz and Bertolani, 2009
Semliki	gallery forest, woodland, grassland/swamp	Samson and Hunt, 2012
Issa	gallery forest (1.5%), miombo woodland (90.5%), grassland/swamp (8%)	This study; Hernandez-Aguilar, 2009

Detailed descriptions of habitat use by chimpanzees were only available for the study sites of Assirik and Fongoli. In a study of chimpanzee nest distribution at Assirik, 56% of nests were found in woodland, 32% in forest, and 12% in grassland habitats, indicating the greatest nest use in woodland. However, relative to habitat availability, more nests were found in forest than would be expected, particularly during the dry season. Most direct observations of chimpanzees during the middle and late dry seasons also occurred in gallery forest (McGrew et al., 1981; Baldwin et al., 1982). Pruetz and Bertolani (2009) found similar patterns of habitat use by Fongoli chimpanzees; 65% of nests were found in woodland, 23% in grassland, and 8% in forest. Again, relative to habitat availability, forest was the preferred habitat for chimpanzee nests. Chimpanzees were also found to use forested habitats almost twice as much during the dry season as compared to the wet season.

Issa chimpanzees have the same habitat use patterns as those at Assirik and Fongoli; in general, Issa chimpanzees are encountered (directly and indirectly) more often in woodland than forest, but they are found in forest much more than expected based on the availability of each habitat type. Additionally, Issa chimpanzees also use forest habitats more often during the dry season as compared to the wet season. At all three sites, forest habitats offer continuously available water sources and lower temperatures, so it is not surprising that chimpanzees use this habitat more frequently, particularly during the dry season when temperatures are extreme and water is scarce.

DIETARY RESOURCE USE

The number of plant species eaten by chimpanzees at each study site is listed in Table 8-4. Since there are slight differences between the two major chimpanzee study communities at Kibale, dietary resource use of these two communities are described separately. The diet of Issa chimpanzees includes 153 plant species; of the other sites, only Tai and Mahale chimpanzees are known to eat a greater number of plant species. Furthermore, the diet of chimpanzees at Issa includes more than three times the number of plant species reported for the diets of chimpanzees at any of the other dry sites. This suggests that Issa chimpanzees have a broader vegetative diet, particularly compared to other dry-habitat chimpanzees.

Table 8-4
Number of plant species eaten for select chimpanzee study sites; shaded rows are dry sites

Site	**Number of plant species eaten**	**Reference**
Tai	223	Boesch et al., 2006
Kibale- Kanyawara	112	Wrangham et al., 1991
Kibale- Ngogo	126	Potts et al., 2009
Budongo	83	Stumpf, 2011
Gombe	103	Stumpf, 2011
Mahale	198	Matsumoto-Oda and Kasagula, 2000
Assirik	43	McGrew et al., 1988
Fongoli	47	Pruetz, 2006
Semliki	45	Hunt and McGrew, 2002
Issa	153	This study; Hernandez-Aguilar, 2006

At all study sites, chimpanzee diet consists mostly of fruit, but the amounts vary across sites. For example, in a study of Kanyawara chimpanzees, Wrangham et al. (1996) observed chimpanzees eating ripe fruit 64.4% of their total time spent feeding. In a similar study, Potts et al. (2009) observed Ngogo chimpanzees eating ripe fruit 80.5% of their total time spent feeding. Budongo chimpanzees spent between 65% and 71% of their total feeding time eating fruits (Newton-Fisher, 1999 and Tweheyo et al., 2003, respectively), while Gombe chimpanzees spent 63% of their feeding time eating fruits (Wrangham, 1977). While these studies reported on the percent of feeding time devoted towards fruits, other studies have examined the number of feeding observations (instead of time spent feeding) in which fruit was consumed. For example, Fongoli chimpanzees were observed eating fruit during 62.5% of all feeding observations. Similarly, Issa chimpanzees were observed eating fruit during 83% of all feeding observations during this study. This percentage, however, might be artificially inflated for Issa chimpanzees due to an extremely small sample size of observations (i.e., only 23 direct feeding observations).

Of the many species of fruits eaten by chimpanzees, figs (*Ficus* sp.) are an important fruit resource at all study sites. At Kibale, figs comprised 70.6% of all fruit eaten by Kanyawara chimpanzees (Wrangham et al., 1996), while figs comprised 46.6% of all fruit eaten by Ngogo chimpanzees (Potts et al., 2009). The percentage of figs out of all fruit eaten by Issa chimpanzees cannot be calculated from this study, but figs are clearly an important part of their diet, since 55.4% of all fecal samples contained fig seeds. Additionally, Issa chimpanzees ate figs during every month of the year. Chimpanzees at Fongoli and Budongo also consume figs during most or all months of the year (Newton-Fisher, 1999; Tweheyo and Lye, 2003; Pruetz, 2006).

In addition to fruit, the diet of chimpanzees also includes other plant items (e.g., leaves, flowers, bark, etc.) and animal matter, including both invertebrates and vertebrates. Insectivory at most East African chimpanzee sites occurs seasonally (McGrew et al., 1979; McGrew and Collins, 1985), while Fongoli chimpanzees eat invertebrates, particularly termites, throughout the entire year (Bogart and Pruetz, 2008). At Issa, most invertebrates were found in fecal samples collected during the wet season, but a few samples collected during the dry season also contained termites. A more focused study on the insectivory of Issa chimpanzees is needed to determine whether they follow the seasonal patterns exhibited by other East African chimpanzees, or more closely resemble Fongoli chimpanzees with the consumption of insects throughout the year. During this study, chimpanzees were never observed eating meat, and no vertebrate remains were found in fecal samples. However, this result does not necessarily mean that

Issa chimpanzees never prey upon other animals; many other chimpanzee researchers did not find evidence of meat-eating at their sites until long after their study subjects were well-habituated (e.g., Ghiglieri, 1984; Nishida, 1990; Reynolds, 2005). Furthermore, mammal species that are frequently preyed upon by chimpanzees at other sites can be found at Issa (Uehara, 1997), so the lack of potential prey is not an issue.

SYMPATRIC FAUNA AND INTERSPECIFIC INTERACTIONS

The diversity and abundance of non-chimpanzee fauna greatly influences the ecological role that chimpanzees occupy within their larger faunal communities. Fauna sympatric with chimpanzees can be predators, prey, competitors for spatial and dietary resources, and/or simply be present in the same study area without any positive or negative influences on the chimpanzees.

Potential chimpanzee predators include large carnivores such as leopards, lions, hyenas, and wild dogs. Of the chimpanzee sites compared here, leopards occur at all sites; lions are present at all sites except for Fongoli; hyenas are absent from Semliki, Budongo, and Tai; and wild dogs are only present at Mahale, Assirik, and Issa (T Webster, unpublished data; Piel, 2004; Russak and McGrew, 2008; Stewart, 2011). No evidence of predation upon chimpanzees was found during this study or at most other sites. The exceptions are numerous predation events upon chimpanzees by leopards recorded at Tai (Boesch and Boesch-Achermann, 2000), and evidence of lions preying upon chimpanzees at Mahale (Tsukahara, 1993). Potential prey for chimpanzees include at least 32 species of mammals across study sites (Uehara, 1997), and other animals such as birds, reptiles, and insects. Evidence of hunting by chimpanzees has been found at all of the study sites mentioned above in Tables 8-1 through 8-4, except for Semliki and Issa.

As previously mentioned, most studies of chimpanzee resource competition focus mainly on other primates species. Additionally, these studies are most often limited to dietary competition only. No data were available on the amount of overlap in use of spatial resources between chimpanzees and other fauna for the sites compared here. Overlap in dietary resources has not been examined at all sites, but available information for Mahale, Budongo, and Kibale are presented here. Matsumoto-Oda and Kasagula (2000) found that the diet of Mahale chimpanzees only overlapped 18% with the diet of baboons, but that baboon diets contained 91% of the items found in the chimpanzee diet; no other interspecific dietary comparisons were made. At Budongo, Plumptre (2006) found that the diet of chimpanzees overlapped 50% with the diet of blue monkeys, 45% with the diet of redtail monkeys, and 35% with the diet of black-and-white colobus monkeys. Ghiglieri (1984) found similar amounts of overlap in the diets of chimpanzees and other primates at Kibale; of 50 food types eaten by chimpanzees, baboons overlapped 24%, redtail monkeys 48%, blue monkeys 32% and red colobus 20%. The amount of overlap of chimpanzee diet with that of squirrels, turacos, and hornbills was also calculated (Table 8-5). Ghiglieri's results indicate that these non-primate species are also significant competitors for chimpanzee food items. Unfortunately, while these same animals were present at Issa and observed to eat some of the same plant species as chimpanzees, calculations of dietary overlap could not be calculated due to small sample sizes of direct feeding observations and no collected fecal samples for these species. The amount of overlap in the diet of Issa chimpanzees and other primate species, however, was less than found elsewhere; the diet of redtail monkeys only overlapped with that of chimpanzees by 36.2%, and the diet of baboons overlapped with that of chimpanzees by 11.8%.

Table 8-5
Dietary overlap of chimpanzees and sympatric species at Kibale, as reported by Ghiglieri (1984)

Species	Percent overlap with chimpanzee diet
Baboon	24%
Redtail monkey	48%
Blue monkey	32%
Red colobus	20%
Squirrel	36%
Turaco	16-22%
Hornbill	20%

DISCUSSION

Based on the assumption that resources are more unevenly distributed through space and time in a savanna-woodland environment, Issa chimpanzees were expected to have a broader realized niche as compared to chimpanzees at wetter, more forested sites. Specifically, Issa chimpanzees were expected to use a greater number of available food items (prediction A1), rely on more rare food items (prediction A2), and use a greater number of habitat types (prediction A3). Additionally, more negative interspecific interactions were expected in the forms of both direct and indirect competition (predictions B1 and B2, respectively), and predation (predictions B3 and B4).

Compared to other chimpanzee communities, Issa chimpanzees have a broader diet, specifically in terms of plant species eaten; the diet of Issa chimpanzees included more plant species than six of the eight other chimpanzee communities compared here, supporting prediction A1. Furthermore, fruit seeds found in the fecal samples of Issa chimpanzees represented many species, indicating that time was spent feeding on many different plant species during each month and throughout the year. In contrast, Fongoli and Kibale chimpanzees appear to have a very narrow and non-diverse diet, focusing on only a few key fruit species each month (Wrangham et al., 1996; Pruetz, 2006; Potts et al., 2009). Plant species eaten by Issa chimpanzees were those found only infrequently within focal patches and along phenological transects; therefore, chimpanzees are eating food items that are scarcer throughout the environment, which supports prediction A2. While it is possible that the distribution of plant species within patches and along transects is not truly representative of the plant distribution throughout the study site, it is more likely that Issa chimpanzees are indeed consuming plant species that are not numerous throughout the study area, but are instead more patchily distributed.

Determining whether or not Issa chimpanzees use a greater number of habitat types as compared to other chimpanzees is difficult, particularly due to the differences in habitat classifications across sites. Simplifying habitat types into the gross categories of "forest" and "woodland" allows for some comparisons to be made, and given that Issa chimpanzees are using both woodland and forest instead of limiting their habitat use to only one habitat type, there is at least some support for prediction A3. When disregarding the availability of each habitat type, Issa chimpanzees are using woodland habitats more often than forest. However, Issa chimpanzees are using forested areas much more than would be expected given the limited availability of this habitat type. Use of forest is particularly greater during the dry season as compared to the wet season. This pattern is congruent with habitat use by other dry-habitat chimpanzees (McGrew et al., 1981; Baldwin et al., 1982; Pruetz and Bertolani, 2009). The extreme climatic conditions of these sites (i.e., hot temperatures and scarce water), especially during the dry season, are most likely influencing the habitat use patterns of chimpanzees.

Resource competition between chimpanzees and other fauna was much less than expected. No direct competition was observed during this study, and both spatial and dietary overlap was minimal, contradicting predictions B1 and B2. However, the expectation of high levels of competition was based on the assumption of extremely scarce resources. While each particular plant species may not be abundant throughout the whole study area of Issa, there are numerous food items available year-round. Furthermore, population densities of potential competitors (e.g., other primates and non-primate frugivores) do not appear to be large. Therefore, the expectation becomes one of limited competition only. Compared to other chimpanzee sites, there seems to be a reduced level of competition for dietary resources at Issa, but further investigation into the diets of non-primate frugivores is needed before a final conclusion can be made.

In comparison to other chimpanzee communities, Issa chimpanzees have some attributes that are more similar to other dry sites (e.g., seasonality, annual rainfall, density), and other attributes that are more similar to wet sites (e.g., population size, dietary breadth). Therefore, providing a general description of “dry-habitat chimpanzees” becomes complicated, since there are differences among dry-habitat sites. These results emphasize the need to assess and acknowledge variation within and between populations, especially when attempting to draw conclusions on the population or species level.

CHAPTER 9: CONCLUSIONS AND BROADER IMPLICATIONS

CONCLUSIONS

Chimpanzees are ideal for community ecology research because they are found in a variety of habitats. Across study sites, one finds the necessary variation in both behaviors and environments allowing for the investigation and comparison of the relationships between these factors. There is a wealth of information about chimpanzees living in more closed and/or wetter forested sites, yet little is known about chimpanzees living in very dry savanna-woodland habitats.

My research investigated the occupied niche of chimpanzees (*Pan troglodytes schweinfurthii*) in an open, dry savanna-woodland environment by collecting data on, and examining patterns of, resource use and interspecific interactions. To better elucidate relationships between environment and behavior, data collected at the dry-habitat site of Issa in the Ugalla region of western Tanzania were then also compared with published data from other chimpanzee populations. It has been generally assumed that resources are scarce and patchily distributed in savanna-woodland habitats (e.g., McGrew et al., 1981; Isbell and Young, 1996). Therefore, chimpanzees at Issa were expected to have broader resource use, and therefore a broader niche, than forest chimpanzees, particularly due to increased competition with other fauna for fewer available resources. More specifically, I hypothesized that in comparison to other chimpanzee populations, Issa chimpanzees would: A) use proportionally more spatial and dietary resources that were available to them and B) have relatively more instances of negative interspecific interactions, such as competition and predation.

Despite the extreme environmental conditions of Issa, food resources, including large, fleshy fruits, were available throughout the year. Similar to other populations, Issa chimpanzees consumed mostly fruit, with leaves comprising a smaller percentage of their diet. Issa chimpanzees consumed 153 plant species, the majority of which were found in woodland habitat. This number of consumed species is higher than the number of plant species eaten by chimpanzees at other dry-habitat sites (Hunt and McGrew, 2002; Pruetz, 2006), but falls within the range of other wetter chimpanzee sites (Boesch et al., 2006; Stumpf, 2011). Issa chimpanzees were encountered more often in forest than expected, particularly during the dry season, but were found using woodland habitat for activities such as feeding, traveling, and nesting. These patterns of food availability and habitat use suggest that factors such as sloping terrain and/or the location of water had a greater influence in determining which habitat types were most frequently used by Issa chimpanzees, as compared with resource availability. Previous assumptions that dry-habitat chimpanzee sites have limited resources make these results especially important in re-evaluating researchers' preconceptions about the ecology of such sites, and its resulting influence on animal behavior.

Overall, resource use patterns of non-chimpanzee fauna at Issa were similar to patterns at other sites. Despite chimpanzees and other fauna sharing spatial and dietary resources, there was only nominal overlap. Spatial resources overlapped less than 20% for the majority of Issa fauna, and no animal had more than 40% overlap in diet with chimpanzees. These results indicate low levels of indirect competition between chimpanzees and other fauna. Furthermore, this competition is not from other primates as is usually assumed, but from other frugivores such as birds and squirrels. These results therefore emphasize the need to study communities in terms of dietary or spatial guilds (e.g., frugivores) as compared to phylogenetic groups (e.g., primates). No instances of direct interspecific competition were observed during this study, which further supports the finding that resources are not limited at Issa.

The results of my study have shown that the niche of Issa chimpanzees is not necessarily broader than the niche of other chimpanzee populations, but still differs in important ways (Table 9-1). Issa chimpanzees have a broad diet consisting of a large number of plant species (prediction A1), and this diet is more diverse than the diet of most non-dry-habitat chimpanzee populations (prediction A2). Additionally, as predicted, Issa chimpanzees are using a greater number of habitat types for both food-related and non-food-related activities as compared to other populations (prediction A3), but Issa chimpanzees are still using forested areas much more than expected given the sparse availability of this habitat type. Large amounts of competition (both direct and indirect) for resources by Issa chimpanzees and sympatric fauna were expected, but Issa chimpanzees experience low levels of interspecific competition, which is very different from most other populations (predictions B1 and B2). Furthermore, contrary to my predictions, Issa chimpanzees are not under greater predation pressure from large carnivores, nor do they prey upon other fauna more often, than chimpanzee populations at wetter sites (predictions B3 and B4).

Table 9-1
Summary of the hypotheses and predictions of this study. All hypotheses and predictions are in comparison to chimpanzees from closed, wetter, forested sites

	Supported by results?
<u>Hypothesis A</u>: Issa chimpanzees will use proportionally more spatial and dietary resources	Yes
Prediction A1: Issa chimpanzees will consume more food items	Yes
Prediction A2: Issa chimpanzees will consume more food items that are scarce within the environment	Yes
Prediction A3: Issa chimpanzees will use more habitat types	Yes
<u>Hypothesis B</u>: There will be more negative interspecific interactions at Issa	No
Prediction B1: There will be more direct competition at Issa	No
Prediction B2: There will be more indirect competition at Issa	No
Prediction B3: There will be more predation by Issa chimpanzees	No
Prediction B4: There will be more predation on Issa chimpanzees	No

Increased competition between chimpanzees and sympatric fauna at Issa was expected (i.e., predictions B1 and B2) based on the assumption that resources are more patchily distributed and scarce in a dry savanna-woodland environment (McGrew et al., 1981). However, the results of my study show that resources, particularly dietary resources in the form of fruits and leaves, are available year round and are not scarce at Issa. Therefore, low levels of interspecific competition for these resources, as found in this study, are not surprising. Furthermore, the community dynamics observable in present-day Issa are not necessarily the same as the past ecological relationships of this community. In other words, competition levels could have been higher in the past, causing species to shift their niche space until competition was reduced. Data from previous years demonstrating that current occupied niches differ from earlier niches of species would support this notion of competition in the past, but unfortunately these data are not available.

Although predation was expected to occur more often at Issa (predictions B3 and B4), Issa chimpanzees were not preyed upon. Additionally, no vertebrate remains and only few invertebrate remains were found in Issa chimpanzee fecals indicating very minimal levels of predation by chimpanzees. This is in contrast to most other chimpanzee sites, where chimpanzees have been observed in the roles of both prey of large carnivores and predators of smaller mammals and invertebrates. Further study of Issa chimpanzees is needed before concluding whether the apparent lack of predation at Issa is a realistic phenomenon or simply a result of limited observations.

It is apparent that characterizing the niche of “dry-habitat” (or “savanna”) chimpanzees is just as difficult as generalizing about “forest” chimpanzees. Therefore, it is more informative to describe the characteristics of particular chimpanzee populations, such as “Issa chimpanzees” or “Gombe chimpanzees”. Nonetheless, determining the ecological roles of chimpanzees across study sites enables a better understanding of overall chimpanzee ecology, which can then be used for conservation as well as extrapolated into insights about hominid ecology and evolution.

A complete understanding of the ecological role of chimpanzees, however, requires studies within the context of their larger faunal communities. This, in turn, requires research that encompasses both habitat and sympatric fauna, rather than focusing solely on chimpanzees, as is traditionally done with focal follows. Non-primate species must also not be ignored, as these species can greatly influence the socio-behavioral ecology of primates by competing for food and space. Shifting the research focus to include these potential competitors therefore requires methodological modifications.

Most primatological studies employ methodologies that include actively following the species of interest. However, these focal follows are insufficient for community ecology studies, since they overlook crucial phenomena, such as indirect competition, that occur when the focal species is absent. My study focused instead on multiple daylong observations of distinct resource patches in chimpanzee habitat. This project demonstrated that using patch focals successfully allowed for the collection of data pertaining to multiple socio-ecological aspects of numerous species at the same time. More specifically, patch focals facilitated the observation of all animals within a study area; elucidated resources that are not used by the study species; and were particularly well suited for the particular unhabituated community of Issa.

IMPLICATIONS FOR CONSERVATION

In their book, *Primate Conservation Biology*, Cowlishaw and Dunbar (2000) state that, “a clear understanding of problems and solutions is not possible without first understanding the biology of the systems we are trying to conserve” (p.4). Primates are already known to greatly impact the structure and composition of the habitats in which they live through the use of various dietary and spatial resources, and by interacting with other species, particularly as competitors, predators, and/or prey (Goodall, 2005). However, the specific relationships between primate behaviors and their environments greatly differ between taxa, and even within taxa, across populations of the same species.

Therefore, studies, like this one, that highlight the range of behaviors and environments for a given species are extremely useful for guiding conservation strategies.

Although chimpanzees are ecological generalists, distributed across a wide range of environments with variable ecological conditions, they are listed as “endangered” on the IUCN Red List of Threatened Species due to a “significant population reduction in the past 20 to 30 years…and [probable continuation of this reduction] for the next 30 to 40 years” (Oates et al., 2008). As with other primates, chimpanzee populations are most threatened by the loss of habitat, poaching, and exposure to disease (Cowlishaw and Dunbar, 2000; Caldecott, 2005; Inskipp, 2005). Ongoing civil conflicts in areas where chimpanzees live or in neighboring countries also greatly threaten their survival (Miles et al., 2005).

While Tanzania has many protected areas for fauna, more than half of the country’s chimpanzees live in unprotected areas, putting them at risk for disease exposure, snare injuries, and capture for the black market to be sold for body parts or to become part of the illegal pet trade (Massawe, 1992). Even within protected game reserves and parks, chimpanzees and other animals are still at risk due to high levels of poaching by neighboring villagers (Ngure, 2012). During my study at Issa, which is unfortunately located in an unprotected area, I often came across snares and campsites that were left by poachers (Figure 9-1). Evidence of habitat modification and destruction were also encountered, including the use of man-made fires to clear areas of woodland and the stripping and cutting down of trees for lumber (Figure 9-2).

By understanding how anthropogenic habitat changes will affect the chimpanzees (and other fauna and flora in the area), perhaps measures can be found to lessen their effects. Chimpanzee ecology studies such as this one provide a wealth of information not only about the current status quo of a particular area, but also inform on the possible outcomes as that environment changes. Further, information about any animal's ecological role would be instructive if animals are moving into adjacent areas to avoid anthropogenic effects, or if animals need to be relocated. All are important considerations for conservation policy and procedure.

Figure 9-1. Wire and rope snares that had been collected throughout the study area by myself and field assistants, over a two-day period during the dry season.

Figure 9-2. Example of a tree that has been stripped of its bark (top) and the resultant section of bark (bottom); this process of stripping bark around the entire circumference kills the tree.

It became obvious during my study that local villagers were more hesitant to enter the study area after learning of the presence of researchers; while the study area is not protected under law, it is widely known that hunting is only allowed with permits and in particular locations, so there was a legitimate cause for concern by local poachers of being caught and turned in to the local authorities. A decrease in hunting has also been observed with the presence of researchers and/or research stations at other sites (e.g., N'Goran et al., 2012).

Deterrence of illegal activities by their mere presence is only one way that researchers can help with conservation. The data collected by researchers can be used to create and manage research areas with the aid of local communities and government agencies, particularly by identifying threats and ways to address them. Creation of research areas also brings much-needed funds and attention to these areas and provides the opportunity for locals to be trained as field assistants and researchers (Varty et al., 2005; Redmond and Virtue, 2008; Wrangham and Ross, 2008; Strier, 2011). By collaborating with organizations like the Tanzanian Wildlife Research Institute (TAWIRI) and the Jane Goodall Institute (JGI), my study in particular has contributed to the conservation efforts taking place in the Masito-Ugalla region of Tanzania.

IMPLICATIONS FOR HUMAN EVOLUTION STUDIES

Many reconstructions of paleo-environments are based on the presence or absence of particular fossil fauna (e.g., Olson and Rasmussen, 1986; Plummer and Bishop, 1994; Kappelman et al., 1997; Reed, 1997, 1998, 2002). Presence of similar extant fauna and the relationships between behaviors and environments of extant taxa can be used to formulate hypotheses about the behavior of related extinct taxa in paleo-environments. The extant species chosen to referentially model the behavior of extinct species is most often based on analogy (i.e., similarities in basic characteristics) or homology (i.e., similarities due to a shared phylogeny) (Moore, 1996). Conceptual models based on patterns of variation across sites are also used, but less often than referential (i.e., analogous or homologous) models (Lewin and Foley, 2004).

As our closest living relatives, chimpanzees have often been used as referential models for early hominin ancestors (e.g., Kortlandt, 1983; Susman, 1987; Moore, 1992, 1996; Zihlman, 1996; Zihlman et al., 2004; Knott, 2005; Yamagiwa and Basabose, 2006; Watts, 2008; Hernandez-Aguilar, 2009; McGrew, 2010). Research using chimpanzee models has included topics such as body size, social organization, locomotor and positional behavior, tool-use and other cultural behaviors, and diet. However, determining whether shared attributes between chimpanzees and hominins are due to their shared phylogeny or not can be difficult, especially without considering any other species or taxonomic group. This particular criticism has been brought up numerous times by researchers who are in favor of getting rid of the chimpanzee model for early hominins, particularly because chimpanzees are not "exemplars" of the last common ancestor (e.g., Sayers and Lovejoy, 2008; Sayers et al., 2012). While it is important to avoid the pitfall of *seeming* to claim that early hominins were exactly like chimpanzees, Sayers et al. overlook the usefulness of using chimpanzees as part of conceptual models within an ecological framework.

Early hominins (e.g., *Australopithecus*, *Ardipithecus*) have been reconstructed as large-bodied frugivorous/omnivorous mammals that spent their time on both the ground and in the trees (Moore, 1996; Stern, 2000; Sponheimer and Lee-Thorp, 2003; White et al., 2009; Stanford, 2012). Of extant mammals, this description most closely matches that of the great apes (i.e., orangutans, gorillas, chimpanzees, and bonobos). It is also well agreed upon that early hominins showed a generalized adaptability, living in a wide variety of environments and having broad diets (McKee, 1999; Strait, 2010). Of the extant great apes, only the chimpanzee has been described as an environmental generalist, living in numerous types of environments (Inskipp, 2005). Therefore, understanding the relationships between the behaviors and environments of different chimpanzee populations across study sites *can* inform hypotheses about the community ecology of early hominins, due to the parallels of ecology and presumably behaviors.

Of particular interest to paleoanthropologists is the expansion of early hominins into drier, open habitats, because these habitats are thought to have limited resources, particularly for a large-bodied frugivore. Therefore, studies like this one, that highlight the adaptations of dry-habitat chimpanzees, can elucidate the role of early hominins that lived in similar dry, wooded environments (Andrews, 1989; Stanley, 1992; Kingston et al., 1994; Harris and Cerling, 1995; Leakey et al., 1995; Reed, 1997, 1998, 2002; Potts, 1998; Wynn, 2000; Bobe et al, 2002; Aronson et al., 2008; Le Fur et al., 2009; White et al., 2009). My dissertation research, in particular, demonstrated that resources are not necessarily limited in dry, open environments. Additionally, chimpanzees in such an environment may be using these open wooded habitats as much as they are using forested areas, as in this study. However, not all dry-habitat chimpanzees exhibit the same patterns of habitat use. For example, Schoeninger et al. (1999) found that chimpanzees at Ishasha, a dry, open site in the Democratic Republic of Congo, mostly consumed fruit from forested areas. This contrasts with Issa chimpanzees, whose diet is primarily composed of woodland fruits. Understanding the ecological and behavioral differences between populations of chimpanzees living in similar environments can provide insights about the potential niches (i.e., the fundamental niche) of early hominins. For example, studies focusing on the isotopic analyses of foods consumed by early hominins have found that they were eating foods with C_4 signatures, such as grasses, sedges, and animals that feed on this type of vegetation. In contrast, all chimpanzees studied thus far (even dry-habitat populations) are eating foods with C_3 signatures, such as fruits and flowers (Sponheimer and Lee-Thorp, 2003; Sponheimer et al., 2006). The results of these studies suggest that by shifting to a diet dominated by C_4 foods, as compared to C_3 foods, early australopithecines were able to expand into more open, dry environments while avoiding potential competition with similarly sized frugivorous fauna. By studying the variability in extant chimpanzee community ecology, particularly at dry-habitat sites, researchers will gain a better understanding of the available niches for early hominins and how they might have filled these niches, expanding the range of environments in which they could have survived.

Furthermore, since the faunal assemblages are well-known at many of these hominin sites, levels of potential competition between hominins and other animals can be assessed by comparison with the amounts of competition observed in extant communities with similar taxonomic and ecological compositions. In order to have the data necessary for such comparisons, there needs to be more studies similar to this dissertation, which focuses upon entire faunal communities. Research using the favored methodology of focusing on one or more species of the same phylogenetic group (e.g., primates or ungulates or carnivores) does not provide the depth or range of data required.

Whether to augment conservation strategies, to aid in interpretation and extrapolation of extinct hominin ecological patterns, or simply to expand and enhance our understanding of the ecological role of chimpanzees across all habitat types, the methods and conceptual framework used in my study have proven to be successful and will hopefully become an established approach of future anthropological research.

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APPENDIX A

FAUNA PRESENT AT ISSA

Fauna recorded in Issa during current and previous studies (modified from Hernandez-Aguilar, 2009; Stewart, 2011; C Johnson, unpublished data). Evidence: N-not seen in current study; DO-direct observation; I-indirect evidence (feces, prints, feathers, quills, burrows, vocalizations); C-camera trap photo/video. Category: classification abbreviation used in Chapter 7 of this dissertation. Category letters used to indicate taxa are only assigned to those used in analyses for this study; A: artiodactyl, B: bird of prey, C: (non-herpestid) carnivore, FB: frugivorous bird, H: herpestid, NCP: non-chimpanzee primates, O: other, R: rodent. Taxonomy based on Groves, 2001; Groves and Grubb, 2011.

Class **Order** *Species*	Common name	Evidence	Category
Mammalia			
Artiodactyla			
Alcelaphus lichtensteini	Lichtenstein hartebeest	DO, I, C	A
Philantomba monticola	Blue duiker	DO, I, C	A
Damaliscus lunatus topi	Topi	N	
Hippotragus equinus	Roan antelope	DO, I, C	A
Hippotragus niger	Sable antelope	N	
Kobus ellipsiprymnus	Defassa waterbuck	DO, C	A
Oreotragus oreotragus	Klipspringer	DO, I, C	A
Ourebia ourebi	Oribi	N	
Phacochoerus africanus	Warthog	DO, C	A
Potamochoerus larvatus	Bushpig	DO, I, C	A
Redunca redunca	Bohor reedbuck	DO, I	A
Madoqua kirki	Kirk's dikdik	N	
Sylvicapra grimmia	Grey (bush) duiker	DO, I, C	A
Syncerus caffer	African buffalo	I, C	A
Taurotragus oryx	Eland	I	A
Tragelaphus scriptus	Bushbuck	DO, I, C	A
Carnivora			
Aonyx capensis	African clawless otter	I	C
Bdeogale crassicauda	Bushy-tailed mongoose	I, C	H
Canis mesomeles	Black-backed jackal	DO, I	C
Civettictis civetta	African civet	I, C	C
Crocuta crocuta	Spotted hyena	I	C
Felis serval	Serval	C	C
Felis sylvestris	African wild cat	I	C
Genetta genetta	Common genet	I, C	C
Helogale parvula	Dwarf mongoose	DO, I, C	H
Herpestes ichneumon	Lesser mongoose	DO, I	H
Herpestes naso	Long-snouted mongoose	C	H
Herpestes sanguinea	Slender mongoose	C	H
Lycaon pictus	East African wild dog	N	
Mellivoria capensis	East African honey badger	I, C	C

Class **Order** *Species*	Common name	Evidence	Category
Carnivora (cont'd)			
Panthera leo	Lion	I, C	C
Panthera pardus	Leopard	DO, I, C	C
Hyracoidea			
Dendrohyrax arboreus	Tree hyrax	DO, I	O
Heterohyrax brucei	Yellow spotted hyrax	DO, I, C	O
Lagomorpha			
Lepus capensis	Cape hare	DO	O
Macroscelidea			
Elephantulus sp.	Elephant shrew	C	O
Rhynchocyon cirnei	Chequered elephant shrew	DO, C	O
Perissodactyla			
Equus quagga burchelli	Zebra	N	
Pholidota			
Smutsia temminckii	Ground pangolin	I, C	O
Primates			
Chlorocebus aethiops	Vervet monkey	DO, I, C	NCP
Cercopithecus ascanius	Red-tail monkey	DO, I, C	NCP
Cercopithecus mitis	Blue monkey	DO, I	NCP
Galago senegalensis	Senegal galago	DO, I, C	NCP
Otolemur crassicaudatus	Greater galago	DO, I, C	NCP
Pan troglodytes schweinfurthii	Eastern chimpanzee	DO, I, C	Pan
Papio cynocephalus	Yellow baboon	DO, I, C	NCP
Procolobus tephrosceles	Red colobus	DO, I	NCP
Proboscidea			
Loxodonta africana	African bush elephant	N	
Rodentia			
Cricetomys sp.	Giant pouched rat	DO, C	
Gerbillus sp.	Gerbil	DO	
Heliosciurus sp.	Sun squirrel	DO	R
Hystrix africaeaustralis	Porcupine	I, C	R
Paraxerus cepapi	Smith's bush squirrel	DO	R
Protoxerus stangeri	Giant forest squirrel	DO	R
Thryonomys sp.	Cane rat	DO, C	
Tubulidentata			
Orycteropus afer	Ant-bear (aardvark)	I	O

Class Order *Species*	Common name	Evidence	Category
Aves (Birds)			
Apodiformes			
Apus apus	Eurasian swift	DO	
Bucerotiformes			
Bucorvus leadbeateri	Southern ground hornbill	DO, I	FB
Ceratogymna bucinator	Trumpeter hornbill	DO, I	FB
Tockus nasutus	African grey hornbill	DO, I	FB
Caprimulgiformes			
Caprimulgus eurpaeus	Fiery-necked nightjar	DO	
Caprimulgus pectoralis	Freckled nightjar	DO	
Caprimulgus tristigma	Eurasian nightjar	DO	
Macrodipteryx vexillaria	Pennant-winged nightjar	DO	
Charadriiformes			
Vanellus senegallus	African wattled lapwing	DO	
Vanellus spinosus	Spur-winged lapwing	DO	
Coliiformes			
Colius striatus	Speckled mousebird	DO	
Columbiformes			
Treron calvus	African green pigeon	DO, I	FB
Turtur chalcospilos	Emerald-spotted wood dove	DO, I	FB
Streptopelia capicola	Ring necked dove	DO	FB
Coraciiformes			
Alcedo quadribrachys	Shining-blue kingfisher	DO	
Coracias caudate	Lilac-breasted roller	DO	
Corythornis cristata	Malachite kingfisher	DO	
Eurystomus gularis	Blue-throated roller	DO	
Halcyon leucocephala	Giant kingfisher	DO	
Megaceryle maxima	Grey-headed kingfisher	DO	
Phoeniculus damarensis	Green wood-hoopoe	DO	
Rhinopomastus cyanomelas	Common scimitarbill	DO	
Falconiformes			
Aquila rapax	Tawny eagle	DO	B
Aviceda cuculoides	African cuckoo-hawk	DO	B
Buteo buteo	Common buzzard	DO	B
Gypohierax angolensis	Palm-nut vulture	DO, I	B
Milvus migrans	Black kite	DO	B
Polyboroides typus	African harrier-hawk	DO, I	B
Terathopius ecaudatus	Bateleur	DO, I	B

Class **Order** *Species*	Common name	Evidence	Category
Galliformes			
Francolinus shelleyi	Shelley's francolin	DO, I	
Numida meleagris	Helmeted guineafowl	DO, I	
Musophagiformes			
Musophaga rossae	Ross's turaco	DO, I	FB
Tauraco schalowi	Schalow's turaco	DO, I	FB
Passeriformes			
Alethe poliocephala	Brown-chested alethe	DO	
Batis molitor	Chin-spot batis	DO	
Cinnyricinclus leucogaster	Violet-backed starling	DO	
Dicrurus adsimilis	Common drongo	DO	
Eulectes macrourus	Yellow-mantled widowbird	DO	
Euplectes orix	Southern red bishop	DO	
Lagonosticta senegala	Red-bellied firefinch	DO	
Motacilla aguimp	African pied wagtail	DO	
Monticola saxatillis	Common rock thrush	DO	
Myrmecocichia arnoti	White-headed black chat	DO	
Oriolus auratus	African golden oriole	DO	
Ploceus cucullatus	Black-headed weaver	DO	
Ploceus ocularis	Spectacled weaver	DO	
Poicephalus meyeri	Brown parrot	DO, I	FB
Prionops plumata	White-crested helmet-shrike	DO	
Pycnonotus pycnonotus	Common bulbul	DO, I	FB
Terpsiphone viridis	African paradise-flycatcher	DO	
Pelecaniformes			
Bostrychia hagedash	Hadada ibis	DO, C	
Scopus umbretta	Hamerkop	DO	
Piciformes			
Campthera cailliautii	Green-backed woodpecker	DO	
Dendropicos namaquus	Bearded woodpecker	DO	
Indicator indicator	Greater honeyguide	DO	
Strigiformes			
Glaucidium capense	African barred owlet	DO	
Reptilia			
Testudines			
Kinixys spekii	Speke's hing-back tortoise	DO	
Pelomedusa subrufa	African helmeted turtle	DO	

Class **Order** *Species*	Common name	Evidence	Category
Squamata			
Lacertilia (sub-order)			
Acanthocercus atricollis	Blue-headed tree agama	DO	
Agama agama	Red-headed rock agama	DO	
Chamaeleo gracilis	Slender chameleon	DO	
Varanus niloticus	Nile monitor	DO	
Scinomorpha (sub-order)			
Chamaesaura anguina	Highland grass lizard	DO	
Gerrhosaurus nigrolineatus	Black lined plated lizard	DO	
Serpentes (sub-order)			
Amblyodipsas polylepis	Common purple-glossed snake	DO	
Aparallactus sp.	Centipede-eater	DO	
Atheris rungweensis	Rungwe bush viper	DO	
Bitis arietans	Puff adder	DO	
Causus rhombeatus	Rhombic night adder	DO	
Crotaphopeltis hotamboeia	White lipped snake	DO	
Dendroaspis polyepis	Black mamba	DO	
Dispholidus typus	Boomslang	DO	
Hemirhagerrhis nototaenia	Bark snake	DO	
Naja nigricollis	Black-necked spitting cobra	DO	
Philothamnus heterolepidotus	Slender green snake	DO	
Philothamnus punctatus	Speckled green snake	DO	
Philothamnus semivariegatus	Spotted bush snake	DO	
Psammophis mossambicus	Olive sand snake	DO	
Python sebae	African rock python	DO	
Telescopus semiannulatus	Tiger snake	DO	
Thelotornis kirtlandii	Forest vine snake	DO	
Scleroglossa (sub-order)			
Hemidactylus mabouia	Tropical house gecko	DO	
Lygodactylus gutturalis	Chevron-throated dwarf gecko	DO	
Trachylepis brevicollis	Short-necked skink	DO	
Trachylepis maculilabris	Speckle-lipped skink	DO	
Trachylepis margaritifera	Rainbow skink	DO	

Class **Order** *Species*	Common name	Evidence	Category
Scleroglossa (cont'd)			
Varanus niloticus	Nile monitor	DO	
Amphibia			
Anura			
Hildebrandtia ornate	African ornate frog	DO	
Tomopterna cryptotis	Common sand frog	DO	
Xenopus muelleri	Muller's Platanna	DO	

APPENDIX B

PLANT SPECIES AT ISSA

Plant species recorded in Issa during current and previous studies (compiled from Hernandez-Aguilar, 2006 and unpublished data from A Hernandez-Aguilar, C Johnson, AK Piel, FA Stewart, S Tapper). "X" in last three columns indicate plant species is eaten by *Pan troglodytes* (chimpanzee), *Papio cynocephalus* (baboon), or *Cercopithecus ascanius* (redtail monkey).

Family *Species*	Eaten by *Pan*?	Eaten by *Papio*?	Eaten by *Cercopithecus*?
Acanthaceae			
Acanthus ueleensis			
Duosperma densiflorum			
Mellera lobulata			
Metarungia pubinervia			
Thunbergia alata			
Amaryllidaceae			
Hypoxis sp.			
Anacardiaceae			
Lannea edulis			
Lannea schimperi			
Lannea schweinfurthii	X		
Mangifera indica	X		
Ozoroa insignis			
Pseudospondias microcarpa			
Rhus longipes			
Rhus pyroides			
Sclerocarya birrea	X		
Scelrocarya caffra			
Sorindeia winkleri			
Trichoscypha ulugurensis			
Anisophylleaceae			
Anisophyllea boehmii	X		
Annonaceae			
Annona senegalensis	X	X	
Artabotrys monteiroae			
Artabotrys stolzii			
Hexalobus monopetalus	X		
Monanthotaxis discrepantinervia			
Monanthotaxis poggei	X	X	
Monanthotaxis sp.			
Monodora angolensis			
Uvaria angolensis	X		
Uvaria sp.	X		X
Xylopia sp.			
Apiaceae			
Steganotaenia araliacea			

Family *Species*	Eaten by *Pan*?	Eaten by *Papio*?	Eaten by *Cercopithecus*?
Apocynaceae			
Acokanthera schimperi			
Ancylobotrys sp.			
Carissa spinarum	X		
Dictyophleba lucisa			X
Diplorhynchus condylocarpon	X	X	
Holarrhena pubescens			
Landolphia owariensis	X		
Landolphia sp.	X	X	
Pleiocarpa sp.			
Rauvolfia caffra			
Saba comorensis	X	X	
Tabernaemontana pachysiphon			
Thevetia peruviana			
Araceae			
Amorphophallus goetzei			
Borassus aethiopum	X		
Araliaceae			
Cussonia arborea			
Arecaceae			
Borassus aethipum			
Phoenix reclinata			
Aselepiadaceae			
Pachycarpus sp.			
Raphionacme welwitschi	X		
Tacazzea apiculata			
Asteraceae			
Aspilia pluriseta	X		
Crassocephalum picridifolium			
Dicoma anomala			
Erythrocephalum longifolium			
Erythrocephalum scabrifolium			
Guizotia scabra	X		
Melanthera pungens			
Melanthera scandens			
Vernonia bellinghamii			
Vernonia sp.			
Bignoniaceae			
Kigelia africana			
Markhamia obtusifolia			
Markhamia zanzibarica			
Stereospermum kunthianum			

Family *Species*	Eaten by *Pan*?	Eaten by *Papio*?	Eaten by *Cercopithecus*?
Boraginaceae			
Cordia sp.	X		
Ehretia cymosa			
Trichodesma zeylanicum	X		
Burseraceae			
Commiphora africana			
Commiphora eminii			
Commiphora sp.			
Capparaceae			
Maerua sp.			
Ritchiea albersii			
Ritchiea sp.			
Celastraceae			
Maytenus senegalensis	X		
Maytenus undata			X
Pleurostylia africana	X		
Chrysobalanaceae			
Parinari curatellifolia	X		
Clusiaceae			
Garcinia buchananii			
Garcinia huillensis	X	X	X
Harungana madagascariensis			
Psorospermum febrifugum			
Combretaceae			
Combretum collinum			
Combretum molle			
Combretum pentagonum			
Combretum zeyheri			
Terminalia mollis			
Terminalia sericea			
Connaraceae			
Rourea orientalis			
Rourea thomsonii	X		
Convolvulaceae			
Ipomoea prismatosyphon			
Lepistemon owariense			
Cyperaceae			
Abildgaardia ovata			
Bulbostylis pilosa			
Cyperus digitatus			
Cyperus exaltatus			
Cyperus niveus			

Family *Species*	Eaten by *Pan*?	Eaten by *Papio*?	Eaten by *Cercopithecus*?
Cyperaceae (cont'd)			
Cyperus platycaulis			
Fuirena sp.			
Dichapetalaceae			
Dichaptalum fadenii	X		
Dilleniaceae			
Tetracera masuiana			
Dioscoreaceae			
Dioscorea cochleariapiculata			
Dipterocarpaceae			
Monotes adenophyllus			
Monotes sp.			
Ebenaceae			
Diospyros gabunensis			
Diospyros zombensis			
Euclea divinorum			
Euclea natalensis			
Erythroxylaceae			
Erythroxylum emarginatum			
Euphorbiaceae			
Acalypha chirindica			
Acalypha ornate			
Alchornea laxiflora			
Antidesma venosum	X		
Argomuellera macrophylla			
Bridelia micrantha			
Croton sp.			
Drypetes gerrardii			
Erythrococca sp.			
Hymenocardia acida			
Margaritaria discoidea			X
Neoboutonia sp.			
Phyllanthus engleri			
Phyllanthus muellerianus			
Pseudolachnostylis maprouneifolia	X		
Thecacoris lucida			
Uapaca kirkiana	X	X	
Uapaca nitida	X	X	
Fabaceae			
Acacia polyacantha			
Adenodolichos kaessneri			
Aeschynomene leptophylla			

Family *Species*	Eaten by *Pan*?	Eaten by *Papio*?	Eaten by *Cercopithecus*?
Fabaceae (cont'd)			
Aeschynomene mossoensis			
Aeschynomene multicaulis			
Afzelia quanzensis			
Albizia adianthifolia			
Albizia amara			
Albizia antunesiana			
Albizia zygia			
Aphanocalyx richardsiae			
Baphia capparidifolia			
Baphia descampsii			
Bauhinia thonningii	X		
Bobgunnia madagascariensis			
Brachystegia angustistipulata			
Brachystegia boehmii			
Brachystegia bussei	X	X	
Brachystegia longifolia	X		
Brachystegia manga			
Brachystegia microphylla			
Brachystegia spiciformis	X	X	
Brachystegia utilis	X	X	
Burkea africana			
Craibia grandiflora			
Cryptosepalum exfoliatum			
Dalbergia fischeri	X		
Dalbergia malangensis			
Dalbergia nitidula			
Dichrostachy cinerea			
Dolichus kilimandscharicus	X		
Droogmansia pteropus			
Eriosema parviflorum			
Erythrina excelsa			
Erythrophleum africanum			
Indigofera podocarpa			
Indigofera rhynchocarpa			
Isoberlinia tomentosa			
Julbernardia globiflora			
Julbernardia paniculata			
Julbernardia unijugata	X		
Kotschya carsonii			
Lonchocarpus capassa			
Mimosa pigra			

Family *Species*	Eaten by *Pan*?	Eaten by *Papio*?	Eaten by *Cercopithecus*?
Fabaceae (cont'd)			
Piliostigma thonningii			
Pericopsis angolensis			
Pterocarpus angolensis			
Pterocarpus tinctorius	X		
Tamarindus indica			
Tessmannia dewildemaniana			
Vigna monophylla	X		
Flacourtiaceae			
Buchnerodendron lastiocalyx			
Flacourtia indica	X	X	X
Homalium sp.			
Phylloclinium paradoxum			
Rawsonia reticulata			
Scolopia sp.			
Hippocrateaceae			
Salacia erecta			
Iridaceae			
Gladiolus atropurpureus			
Gladiolus dalenii			
Lamiaceae			
Ocimum capitatum			
Ocimum fimbriatum			
Plectranthus sp.			
Scutellaria violascens			
Lauraceae			
Beilschmiedia ugandensis			
Liliaceae			
Aloe bicomitum			
Chlorophytum vestitum			
Loganiaceae			
Anthocleista schweinfurthii			
Mostuea sp.			
Nuxia sp.			
Strychnos cocculoides	X	X	
Strychnos innocua	X		
Strychnos lucens			
Strychnos panganiensis	X		X
Strychnos potatorum			
Strychnos pungens	X		X
Strychnos spinosa	X		
Strychnos sp.	X	X	X

Family *Species*	Eaten by *Pan*?	Eaten by *Papio*?	Eaten by *Cercopithecus*?
Loranthaceae			
Englerina holstii		X	
Oncocalyx sp.			
Malvaceae			
Hibiscus calyphyllus			
Hibiscus canabirus	X		
Thespesia garckeana	X		
Melastomataceae			
Dissotis sengambiensis			
Meliaceae			
Lepidotrichilia volkensii			
Trichilia dregeana			
Melianthaceae			
Bersama abyssinica			
Menispermaceae			
Stephania abyssinica			
Moraceae			
Dorstenia hildebrandtii			
Ficus cyathistipula			
Ficus exasperata	X		
Ficus ottoniifolia	X		
Ficus sur			
Ficus sycomorus			
Ficus thonningii			
Ficus variifolia	X		
Ficus verruculosa			
Ficus sp.			
Myrtaceae			
Morella serrata			
Syzygium cordatum			
Syzygium guineense	X		
Ochnaceae			
Ochna mossambicensis	X		
Ochna sp.			
Ouratea sp.			
Olacaceae			
Strombosia scheffleri			
Ximenia caffra	X	X	
Oleaceae			
Chionanthus niloticus			
Schrebera trichoclada			

Family *Species*	Eaten by *Pan*?	Eaten by *Papio*?	Eaten by *Cercopithecus*?
Onagraceae			
Epilobium hirsutum			
Ludwigia abyssinica			
Ludwigia leptocarpa			
Opiliaceae			
Opilia celtidifolia	X		
Orchidaceae			
Corymborkis corymbis			
Disa robusta			
Eulophia angolensis			
Habenaria debeerstiana			
Oxalidaceae			
Biophytum umbraculum			
Poaceae			
Brachiaria brizanllianthia	X		
Brachiaria eminii			
Brachiaria serrifolia			
Olyra latifolia			
Setaria megaphylla			
Setaria sphacelata			
Sporobolus sp.			
Polygalaceae			
Carpolobia goetzei	X		X
Securidaca longipedunculata			
Polygonum senegalense			
Proteaceae			
Faurea rochetiana			
Protea sp.			
Pteridophyta			
Asplenium buettneri			
Nephrolepis undulata			
Pellaea angulosa			
Ranunculaceae			
Clematis sp.			
Rhamnaceae			
Ziziphus abyssinica	X		
Rhizophoraceae			
Cassipourea malosana			
Cassipourea sp.			
Rosaceae			
Prunus africana			

Family *Species*	Eaten by *Pan*?	Eaten by *Papio*?	Eaten by *Cercopithecus*?
Rubiaceae			
Aidia micrantha			
Apoclytes climidiata			
Canthium burtii	X		
Canthium lactescens			
Canthium parasiebenlistii			
Canthium sp.	X		
Catunaregam oborali			
Catunaregam spinosa			
Coffea Arabica			
Coptosperma graveolens			
Coptosperma neurophyllum			
Craterispermum schweinfurthii			
Cremaspora triflora			
Crossopteryx febrifuga			
Diodia sp.			
Fadogia ancylantha	X		
Fadogia triphylla	X		
Fadogia quarrei	X		
Galiniera saxifraga			
Gardenia imperialis			
Gardenia ternifolia			
Geophila obvallata			
Heinsenia diervilleoides			
Hymenodictyon floribundum			
Ixora narcissodora			
Keetia ferguinea	X		
Keetia gueinzii	X		
Keetia venosa	X		
Keetia sp.			
Leptactina benguelensis		X	
Multidentia crassa			X
Mussaenda arcuata			
Oxyanthus lepidus			
Oxyanthus speciosus	X		
Pauridiantha paucinervis			X
Pavetta bagshawei			
Pavetta comostyla			
Pavetta schumanniana			
Pentanisia sykesii			
Polysphaeria lanceolata			
Polysphaeria parrifolia			

Family *Species*	Eaten by *Pan*?	Eaten by *Papio*?	Eaten by *Cercopithecus*?
Rubiaceae (cont'd)			
Psychotria eminiana	X		
Psychotria kirkii			
Psychotria pumila			
Psychotria sp.	X	X	
Psydrax livida	X		
Pyrostria sp.			
Rothmannia engleriana			
Rothmannia fischeri			X
Rothmannia mangajal	X		
Rothmannia ravae			X
Rothmannia urcelliformis			
Rothmannia sp.	X	X	X
Rutidea smithii			
Rytigynia olicantha			
Spermacoce sp.			
Tapiphyllum cinerascens			
Tarenna neurphylla			
Tarenna pavettoides			
Teclea nobilis			
Tricalysia coriacea			
Tricalysia pallens			
Tricalysia ruandensis		X	
Tricalysia verdcourtiana			
Vangueria infausta			
Vangueria multidentia			
Vangueria volkensii	X		
Rutaceae			
Toddalia asiatica	X		X
Vepris nobilis			
Vepris sp.			
Zanthoxylum chalybeum			
Sapindaceae			
Allophylus congolanus	X		
Allophylus ferrugineus			
Allophylus richardsiae	X		
Macphersonia gracilis	X		X
Pappea capensis			
Zanha africana	X	X	
Sapotaceae			
Chrysophylum banguelensis		X	
Englerophytum magalismontanum			

Family *Species*	Eaten by *Pan*?	Eaten by *Papio*?	Eaten by *Cercopithecus*?
Sapotaceae (cont'd)			
Manilkara mochisia	X		
Synsepalum passargei			
Scrophulariaceae			
Buchnera sp.			
Cycnium tubulosum			
Smilacaceae			
Smilax anceps	X		
Sterculiaceae			
Cola microcarpa			
Dombeya burgessiae			
Dombeya sp.			
Leptonychia sp.			
Melochia melissifolia			
Ochia bolstii			
Sterculia africana			
Sterculia quinguoloba	X		
Taccaceae			
Tacca leontopetaloides	X	X	
Thymelaeaceae			
Gnidia kraussiana			
Tiliaceae			
Corchorus trilocularis			
Glyphaea brevis			
Grewia bicolor			
Grewia rugosifolia	X	X	X
Grewia stolzii			
Grewia sp.			
Turneraceae			
Tricliceras sp.			
Ulmaceae			
Chaetachme aristata			
Trema orientalis			
Velloziaceae			
Xerophyta scabrida			
Verbenaceae			
Clerodendrum myricoides			
Clerodendrum sp.			
Lantana sp.			
Premna sp.			
Vitex doniana	X	X	
Vitex madiensis			

Family *Species*	Eaten by *Pan*?	Eaten by *Papio*?	Eaten by *Cercopithecus*?
Verbenaceae (cont'd)			
Vitex sp.			
Violaceae			
Rinorea ilicifolia			
Rinorea sp.			
Vitaceae			
Ampelocissus africana	X		
Ampelocissus obtusata	X		X
Cayrattia gracilis			
Cissus cornifolia			
Cissus oliveri	X		
Cissus rubiginosa	X		
Cissus sp.			
Cyphostemma serpens			
Cyphostemma stegosaurus			
Zingiberaceae			
Aframomum mala	X	X	X
Costus macranthus	X		
Renealmia sp.			
Zygophyllaceae			
Balanites sp.			

APPENDIX C

SELECT CAMERA TRAP PHOTOGRAPHS

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Figure C1. Camera trap photo of a blue duiker (*Philantomba monticola*) in forest (credit: UPP/MPI-EVA).

Figure C2. Camera trap photo of a klipspringer (*Oreotragus oreotragus*) in woodland (credit: UPP/MPI-EVA).

Figure C3. Camera trap photo of a bushpig (*Potamochoerus larvatus*) in forest (credit: UPP/MPI-EVA).

Figure C4. Camera trap photo of an adult male bushbuck (*Tragelaphus scriptus*) in woodland (credit: UPP/MPI-EVA).

Figure C5. Camera trap photo of an African civet (*Civettictis civetta*) in forest (credit: UPP/MPI-EVA).

Figure C6. Camera trap photo of a serval (*Felis serval*) in woodland (credit: UPP/MPI-EVA).

Figure C7. Camera trap photo of a common genet (*Genetta genetta*) in woodland (credit: UPP/MPI-EVA).

Figure C8. Screen shot of camera trap video of a leopard (*Panthera pardus*) in woodland, taken in June 2011 (credit: UPP/MPI-EVA).

Figure C9. Screen shot of camera trap video of a ground pangolin (*Smutsia temminckii*) in forest, taken in March 2011 (credit: UPP/MPI-EVA).

Figure C10. Camera trap photo of a porcupine (*Hystrix africaeaustralis*) in forest (credit: UPP/MPI-EVA).

Figure C11. Camera trap photo of an adult female chimpanzee (*Pan troglodytes schweinfurthii*) in forest (credit: UPP/MPI-EVA).

Figure C12. Camera trap photo of an adult female chimpanzee (*Pan troglodytes schweinfurthii*) with dorsal infant in forest (credit: UPP/MPI-EVA).