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The Tall Price of Being Small: The Energetic and Fitness Costs of Interspecific Feeding Competition in Wild Primates

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
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by

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"In all things of nature there is something of the marvelous"
– Aristotle

To my parents, who fostered my curiosity about nature
and encouraged me to follow my dreams.

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Just like a food web, the network of people who influence you, those who support you, cheer you on, and help you overcome giant hurdles, is extensive. Like a chimpanzee on a red-tailed monkey, they might not be aware of the effect they have had on you; still, their impact is immense and life changing.

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ABSTRACT

The Tall Price of Being Small: The Energetic and Fitness Costs of

Interspecific Feeding Competition in Wild Primates

by

Ronnie Bailey-Steinitz

Energy is a fundamental resource that drives biological processes, and how animals acquire and mobilize energy from their environments is essential for their survival and reproductive success. Competition for these limited resources is a near-universal force shaping species interactions and ecological communities, but its intensity and outcomes are difficult to quantify and have been historically under-studied in primates. My research aims to investigate these dynamics by examining how fluctuations in competitive pressure influence food access, foraging behavior, physical condition, and reproduction in red-tailed monkeys (*Cercopithecus ascanius*). Red-tails offer a unique opportunity to study these interactions; they are small-bodied, arboreal and fruit-eating primates, whose physiology and existence among several large and dominant competitors make them particularly vulnerable to the costs of competition. To determine the energetic costs of competition, I studied red-tailed monkeys across three sites in and around Kibale National Park in Uganda with varying degrees of competition from chimpanzees (*Pan troglodytes*), grey-cheeked mangabeys (*Lophocebus albigena*), and blue monkeys (*C. mitis*), their main competitors. Using a combination of observational data, metabolic biomarkers, and remote-sensing tools, I evaluated how these competitors affect red-tail physical condition and reproduction.

In Chapter 2, I examined how fluctuations in fruit availability and the presence of chimpanzees, who are dominant frugivorous competitors and predators of red-tails, influence red-tailed monkeys' foraging and energy balance. I evaluated urinary C-peptide, a non-invasive biomarker of energy balance, from six social groups at Ngogo Research Station in Kibale National Park, against fruit availability, foraging behavior, and fluctuations in competitive pressure from chimpanzees. I found that red-tail energy balance decreases dramatically when chimpanzees are drawn to their home range and limit the red-tails' ability to profit from local resources. Polyspecific association with mangabeys also had a similar effect, but blue monkeys did not, underscoring the complexity of interactions within primate feeding guilds. These findings challenge the assumption that more food automatically leads to better nutritional outcomes for all primates.

Since human-measured fruit availability does not represent what is accessible for these subordinate primates, in Chapter 3, I tested an alternative measure of habitat productivity. I used remote-sensed Enhanced Vegetation Index (EVI) data to predict fruit availability and energy balance in frugivorous primates in tropical rainforests. I performed a lag analysis to test whether EVI minima, which correspond with leaf flushing that occurs approximately 2.5 months before fruiting, predicts red-tail C-peptide. EVI minima correlated with high C-peptide values 96 days (~3 months) later and with increased fruit availability 32 days later (~1 month), establishing a link between remote-sensed measures of habitat productivity and frugivorous primate foraging behavior in biodiverse environments.

Lastly, in Chapter 4, I used a comprehensive metabolic biomarker panel for an in-depth investigation of energy mobilization across a gradient of competitive pressure. Using energy balance (urinary C-peptide), relative muscle mass (creatinine), metabolic rate

(triiodothyronine), ketosis (ketones), and protein catabolism (stable nitrogen isotopes), I identified four distinct metabolic profiles spanning different physical conditions. Groups facing higher competition exhibit prolonged energy deficits compared to those with few or no competitors. Competition had no effect on reproduction, indicating that red-tails prioritize reproduction over long-term physical condition, a strategy consistent with fast-paced life histories.

By integrating physiological, ecological, and technological approaches, this dissertation advances our understanding of how small-bodied primates adapt to competitive pressures in dynamic ecosystems. The findings highlight the critical role of competition in shaping energy allocation strategies and primate life histories, while drawing connections between species-level interactions and intrinsic energy mobilization. This underexplored aspect of primate ecology provides new insights into the complex challenges small primates face in under fluctuating competitive landscapes, with broader implications for conservation efforts in increasingly fragmented habitats.

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1.1 Introduction: Ecological Communities

Energy is the currency connecting all living things, flowing from the environment into individuals and driving the intricate web of life. It has been a main focus in the fields of ecology and evolution since their foundation. At every biological level, energy acquisition and utilization are fundamental processes that sustain life (Odum, 1968), and every living thing has evolved strategies to seek, consume, and utilize energy to maximize fitness by reproducing. Energy moves from the abiotic environment to primary producers, then to herbivores that are eaten by carnivores, who eventually perish and return energy to the system, continuing the cycle. However, ecological communities are not merely a collection of food chains shaped by predator-prey interactions; rather, they are comprised of food webs– intricate networks of species that interact with each other in the same area and influence each other's abundance and distribution, both directly and indirectly. Competitive dynamics are key to shaping these communities (Tilman, 1982). Different species with similar needs fight to attain limited resources like space, light, water, or food. By depleting resources or impeding access to certain areas, competition influences populations by limiting their growth (MacArthur & Levins, 1967) and distribution (Hutchinson, 1959), and by driving critical evolutionary adaptations to minimize the costs it inflicts (Schluter, 2000). Competition can result in shifts in resource use patterns that promote coexistence, or might eventually lead to complete exclusion; in other words, species must adapt or perish.

Nearly every species on earth must compete for limited resources (Connell, 1983) and consequently, the field of ecology, from its scientific roots (Darwin, 1959; Gause, 1934;

Grinnell, 1917; Hutchinson, 1959; Lotka, 1925; Volterra, 1927) to modern research (Chesson, 2000; Connell, 1983; Dayan & Simberloff, 2005; Grant & Grant, 2006; Letten et al., 2017; Tilman et al., 2004; Wisz et al., 2013), is rich with studies of interspecific interactions. Some of the most significant and under-explored topics within the broader field of ecology are those regarding interspecific interactions: the connection between the traits of an individual species and the strength and direction of interspecific interactions; how species traits influence the overall structure of ecological networks; and whether the cumulative impact of numerous weak interactions might outweigh the influence of a few strong ones (Sutherland et al., 2013). These questions become particularly pertinent in the context of primate communities, as coexisting species often occupy overlapping *ecological niches* within complex and competitive *feeding guilds* (see section 3. Primate Feeding Guilds; Kamilar & Ledogar, 2011; van Holstein et al., 2024). Primate communities, especially those in biodiverse regions like tropical rainforests, are shaped by a multitude of factors, including *resource partitioning*, competition for food, predation, and mutualistic relationships. The ability of multiple primate species to coexist in the same habitat - despite overlapping dietary needs - raises important questions about the mechanisms that govern niche differentiation, and determines how many species can coexist in a given area and the impacts of both direct and indirect interactions on these assemblages.

The study of primate behavioral ecology has followed a trajectory distinct from that of other taxa. Primates are exceptionally social animals, often characterized by cohesive groups with long-term, bonded social relationships that are rarely seen in other taxonomic groups (Shultz & Dunbar, 2007). As a result, 50+ years of primate research have given significant attention to these social behaviors, including the complexities of maintaining hierarchies and

relationships within groups, and to a lesser extent, competition for resources between social groups (Isbell & Young, 2002; Koenig, 2002; Silk, 2007; Sterck et al., 1997; Terborgh & Janson, 1986; van Schaik, 1989; Wrangham, 1980). This heavy focus on intraspecific social dynamics has come at the expense of a broader understanding of interspecific interactions. This narrow focus creates a significant gap in the literature, where the impacts of *interspecific feeding competition*, particularly within highly competitive environments like tropical rainforests, remain underexplored.

Of the studies on coexisting primates with overlapping diets (Chivers, 1998; Falótico et al., 2021; Ganzhorn, 1988; Gautier-Hion, 1980; Guillotin et al., 1994; Hladik, 1977; Houle et al., 2006; Kamilar & Ledogar, 2011; Stevenson et al., 2000; Struhsaker, 1978, 1980; Struhsaker & Oates, 1975; Terborgh & van Schaik, 1987; van Holstein et al., 2024; Waser & Case, 1981), none address how competition affects individuals at the most proximate level– i.e., their energy intake, physical condition, and their resulting reproductive success. A more holistic approach is necessary to understand the full spectrum of ecological interactions that shape primate behavior, physiology, and survival. Bridging this gap is crucial because interspecific competition is a nearly ubiquitous force in nature that can drive species distributions, influence evolutionary adaptations, and determine the persistence or decline of a species over time.

The strongest factors that shape a species' ecological role are the characteristics of its environment, the competition it experiences from competitors, and its intrinsic traits (van Holstein et al., 2024). This dissertation introduces novel approaches within the field of primate feeding ecology, designed to address these three components shaping ecological niches in the context of interspecific competition among primates in a tropical rainforest

environment. The costs of competition are notoriously challenging to measure, and as a result, little information exists on its physiological outcomes. To develop a stronger understanding of these relationships, **my first objective was to quantify the effects of feeding competition from a large-bodied competitor on a small-bodied primate** by using a physiological biomarker of energy gain, as a measure of food intake in response to food availability and competitive pressure (Chapter 2). In doing so, I discovered that the traditional methods of measuring food availability, a significant component of most studies of primate feeding ecology, do not accurately represent what is actually accessible to species that are low-ranked in the competitive hierarchy. Therefore, **my next goal was to test the effectiveness of a remote-sensed vegetation index, an alternative and more objective measure of habitat quality, as a predictor of primate foraging behavior** (Chapter 3). Finally, to gain a more comprehensive perspective on the *energetic costs* of competition, **I set to assess whether strong competition could lead to prolonged deficits that affect physical condition and reproduction** by evaluating a panel of metabolic biomarkers showcasing different aspects of energy mobilization (Chapter 4).

The field of community ecology investigates sets of species that coexist in a geographic area, with a strong focus on the interactions among them (Gee & Giller, 1987; Guillaumet & Russell, 2022; Kronfeld-Schor et al., 2017; Svenning et al., 2014). Species might depend on one another for food or protection, among other things, so the biogeography of one species can be strongly influenced by the distribution of another (Lehman & Fleagle, 2006). When two or more species pursue the same resources, the species that better acquires or better utilizes them will outcompete others (Gause, 1934; Hardin, 1960; Pocheville, 2015). As a result, these strong asymmetric outcomes may lead to *competitive exclusion*, whereby out-

competed species are prevented from occupying certain areas (Gause, 1934; Lotka, 1925; Volterra, 1928). To persist in such areas of overlap, species must adapt to reduce the costs of competition (see section 3.1). A comprehensive assessment of primate feeding competition across ecological scales is urgently needed to provide insights into how primates and other species have evolved to coexist in environments where resources are limited and competition is intense. By integrating studies of interspecific competition with those of intraspecific dynamics, we can develop a more complete understanding of the factors that influence primate community structure, species interactions, and individual fitness.

Primate communities can help explore these topics because they serve as models for other animal communities. Primates are some of the most numerous and well-studied animals (Burgin et al., 2018; Chatterjee et al., 2009), so there is a wide breadth of knowledge about their evolution, ecology, behavior, and physiology, as well as their similarities to other animals. Primates boast an impressive array of diets, behavioral strategies, and ecological roles, and different species within this order reflect species across a variety of non-primate taxa (Chivers, 1998; Strier, 2016). They have undergone several unique radiations, which have led to their remarkable flexibility, coexistence patterns, and prevalence in many habitat types and across environmental gradients (Lehman & Fleagle, 2006; Reed & Bidner, 2004).

Most primates are members of tropical rainforest *food webs*. Biotic networks in tropical environments are particularly complicated because of their exceptionally high biomass and diversity (Reagan & Waide, 1996). Most food web interactions occur between *trophic levels* and represent relationships between consumers and their food. Some of these interactions have evolved to become mutualistic, such as animals who are plant pollinators and seed-dispersers (Patiny, 2012), while others establish asymmetric benefits to one trophic level over

the other, such as carnivores preying on herbivores (Chapin et al., 2002). Primates comprise a large proportion of frugivore biomass in tropical forests, making them an essential part of this coevolutionary process (Chapman, 1995).

Temporal and spatial fluctuations in the availability of resources further complicate our understanding of primate community dynamics. Environmental fluctuations can lead to shifts in competitive pressure, alter the strength and nature of species interactions, and influence reproductive success and survival rates across species. Acquiring food is a ubiquitous ecological constraint influencing wild primate populations, affecting both individual fitness and population density and distribution (Emery Thompson et al., 2012; Isbell, 1991; Terborgh & Janson, 1986; van Schaik, 1989) and therefore acts as a selective force on primate physiology, ecology, behavior, and social organization (Chapman et al., 2012).

1.2 Primate Communities

Several aspects of primate food webs are yet to be fully addressed: e.g., identifying the mechanisms that determine how many species can coexist in a given area, and at what abundance (i.e., the carrying capacity of the environment); the nature and impact of indirect interactions; the relative roles of trophic versus non-trophic interactions in shaping community composition; and the effects of spatial and temporal environmental heterogeneity on diversity at various scales (Sutherland et al., 2013). Concentrating research efforts on these topics can aid not only in better understanding the evolutionary and ecological mechanisms that govern these natural systems but can also help prioritize areas for future conservation efforts (Wang et al., 2024; White et al., 2006).

1.2.1 Biogeography and Evolutionary Dynamics

Shared biogeographic history and evolutionary processes play a substantial role in shaping primate community structure (Fleagle & Mittermeier, 1980; Reed & Fleagle, 1995; Webb et al., 2002). The diversification and specialization of primate communities, such as those in eastern Madagascar, often reflect functional groups of omnivores, frugivores, and folivores, with species filling adaptive gaps following extinctions or climatic changes (Ganzhorn, 1997). These communities are shaped by evolutionary niche dynamics, with phylogenetic and natural history playing crucial roles in species adaptations and their relationships with other species (Webb et al., 2002; Desdevises et al., 2003; Wiens & Graham, 2005). Historical contingencies, including migration, speciation, extinction, and resource partitioning, strongly influence the size, structure, and dynamics within primate communities. For instance, ancestral primates colonization events led to the unique and diverse primate communities observed today, such as the diversification of strepsirrhines in Madagascar (Herrera, 2017) and the distinct community composition in the Neotropics following the arrival of haplorrhines (Tejedor, 2008). In contrast, African and Asian primate communities were shaped by multiple migrations between and within the continents, resulting in dynamic, yet similar communities (Reed & Bidner, 2004). These historical trajectories are evident in insular communities, which often comprise discrete subsets of species from larger, more diverse communities, influenced by factors like differential colonization, range distribution, and extinction risks related to habitat size and isolation (Patterson & Atmar, 1986; Boecklen, 1997; Ganzhorn, 1998).

The interactions within communities occur on both evolutionary and ecological timescales. Evolutionary processes shape species' traits, influencing their ranges and

community richness (Wiens & Donoghue, 2004), while ecological interactions impact the intensity of species interactions within shorter timeframes (Reed & Bidner, 2004). Historical competitive interactions can leave a lasting imprint on present-day species distributions and ecological niches, even when direct competition is no longer observable, a phenomenon called "the ghost of competition past" (Connell, 1980). This idea highlights the importance of considering not just current interspecific interactions but also the historical contingencies that have shaped primate communities over time. The absence of certain species from seemingly suitable habitats could result from past competitive events (Kamilar & Ledogar, 2011; Segre et al., 2016), underscoring the relationship between past and present ecological dynamics. Biogeographical patterns reveal how historical competition, coupled with evolutionary and environmental factors, has molded the unique assemblages of primate species across different regions.

Primates have different roles in their communities. Most engage in feeding competition with other species (Schreier et al., 2009); some prey upon small vertebrates and insects (Chivers, 1998) or even larger prey (e.g., Harding, 1975; Mitani & Watts, 2001), and some are preyed upon by other primate species (Teelen, 2007). Primates are host to rich communities of parasites (Nunn et al., 2004) and likely originated and coevolved alongside flowering and fruiting trees (Sussman, 1991), which have become a primary food source for many primate species (Lambert, 2010; Lambert & Rothman, 2015). Because they hold diverse and important roles in their habitats, studying the relationships between primates and their environments can help fill the gaps in our understanding of complex community dynamics (Reed & Bidner, 2004).

1.2.2 Environmental Influences on Primate Communities

The most fundamental determinants of species distributions are *abiotic factors*, such as weather and nutrient cycling, which shape habitats and their productivity, and consequently, also the interactions among their animal inhabitants (Chase et al., 2002; Connell, 1980; Hutchinson & MacArthur, 1959). Seasonal changes in these abiotic factors can affect primates directly. For example, primate species in both cold (Japanese macaques; *Macaca fuscata*) and warm environments (mantled howlers; *Alouatta palliata*) experience seasonal changes in thyroid hormone levels to aid in *thermoregulation* (Thompson et al., 2017). Thermoregulation is energetically costly, and energy spent on maintaining body temperature cannot be spent on other physiological functions like reproduction or growth (Pontzer, 2015). Abiotic factors also affect primates indirectly by moderating food availability and influencing interspecific interactions (McLester et al., 2019; van Schaik & Brockman, 2005). Chimpanzee (*Pan troglodytes*) daily activity and travel distance are affected directly by seasonal fluctuations in temperature (Kosheleff & Anderson, 2009) and also indirectly through the influence of climate and weather on fruit production, which in turn determines foraging behavior (Takemoto, 2004). Considering their dominant nature, seasonal changes in the ranging patterns of chimpanzees would almost certainly affect their smaller competitors, too (see Chapter 2). Through such mechanisms, *biotic interactions* also undergo seasonal changes. Primary productivity, which is strongly influenced by climate and weather patterns, plays a role in determining the richness and biomass of primate communities (Ganzhorn, 1997; van Schaik et al., 2005). Some primates depend on key resources like insects during fruit-scarce periods (Terborgh, 2014), which can limit population biomass and, therefore, its effects on other species (Marshall et al., 2009).

The physical aspects of habitats, including their size, structure, and connectivity, play a critical role in shaping ecological communities. In tropical regions, where vegetation ranges from evergreen rainforests to semi-deserts, the duration and intensity of seasons influence habitat structure and, consequently, the niche characteristics and adaptations of its inhabitants. Longer dry seasons lead to declines in forest canopy complexity, species richness, and connectivity, forcing primates to adapt their locomotion and dietary habits to less connected canopies and more open understories. These structural changes result in larger group sizes in more open environments, as larger groups reduce individual *predation risk* (Dunbar, 1988; Terborgh & Janson, 1986; van Schaick, 1983). Additionally, forest structure influences the productivity and quality of food resources, with evergreen forests producing energy-rich fruits and deciduous forests offering nutrient-rich leaves, which in turn affects the biomass and foraging niches of primate communities (Aerts & Chapin, 2000). Larger forests, especially in tropical regions, support higher species diversity and more complex primate communities due to their greater productivity (Harcourt & Schreier, 2009). Rainforests, with their high species richness and pronounced latitudinal gradients in dispersal limitation, are particularly valuable for studying these dynamics. The specialization of primates in tropical regions, along with their latitudinal gradient in dispersal abilities (Beaudrot et al., 2014), contributes to smaller geographical ranges and shapes community composition (known as the "Rapoport Effect"; Rapoport, 2013).

The shape, size, and type of the habitat give rise to the number, size, and characteristics of ecological niches within a habitat, which in turn determine the principles of interactions among its inhabitants. Species coexistence follows particular patterns that are influenced by historical and the aforementioned environmental factors (Elton, 1927; Gleason, 1939).

Community structure can be explained using two opposing views. The closed concept suggests that communities are shaped by specific sets of species that interact within defined and clear habitat types, constrained by the environment and its extrinsic factors (such as climate and nutrient cycles; Clements, 1936). Conversely, the open concept suggests that community structure is the sum total of the interactions between species and each species' adaptations. It proposes that the immigration of species and variability in the environment define communities, not the particular habitat type (Gleason, 1939). Hypotheses about primate origins allude to both of these views. Rainforest habitats are typically *vertically stratified*, which allowed the small-bodied ancestors to forage for fruits and insects on smaller, terminal branches (Sussman, 1991), subsequently shaping arboreal ecological niches. These adaptations remain important for modern primates, most of which inhabit tropical forest environments (Reed & Fleagle, 1995).

As the environment shapes the habitats and complexity of primate communities, they also interact with intrinsic species traits to define the ecological niches occupied by different primates. Understanding how these niches are formed and maintained requires a closer examination of the interspecific interactions within these communities. The interplay between competition, resource use, and predation not only defines a species' niche but also influences how multiple species coexist within overlapping habitats.

1.2.3 The Ecological Niche and Competition

Different types of interspecific interactions coalesce to define a species' ecological niche. In primate communities, the concept of the ecological niche is especially crucial for understanding how multiple species coexist within a habitat. Pioneering efforts formally

defined the ecological niche as a multi-dimensional space that denotes the conditions an organism actually lives in (its realized niche; Hutchinson, 1957), or could potentially live in (its fundamental niche; Hutchinson, 1965). The three main components that shape ecological niches are intrinsic traits, environmental conditions, and competition from other species (van Holstein et al., 2024). These factors hold true for primates, too, although the social dynamics that characterize most primates have become an integral part of the species' ecological niche. For example, a species might evolve to have larger social groups to protect itself from predators (Janson & Goldsmith, 1995), and the resulting social dynamics within the group determine the amount and types of foods individuals can access (Silk, 2007). However, because a niche can be extraordinarily complex, encompassing innumerable ecological, geological, physiological, and behavioral parameters, researchers often focus on specific aspects of a niche at a time. Due to the historically strong emphasis on the connection between food abundance and distribution and primate social behavior and organization (Janson & van Schaik, 1988; van Schaik, 1989; Wrangham, 1980), studying the primate dietary niche– i.e., their range and variation of food consumption and feeding behavior–has become a focal point in studies of wild primates (Kamilar & Ledogar, 2011; Machado et al., 2023; Raubenheimer et al., 2015; Schreier et al., 2009). Primates consume a diverse range of foods, including fruits, leaves, invertebrates, and occasionally vertebrates, with their dietary habits providing crucial insights into their life history, ecology, and behavior and informing both conservation and captive care practices (Rothman et al., 2013).

One critical factor that influences an organism's niche is its body size, as it is closely tied to energetic requirements. Larger-bodied primates, such as gorillas (*Gorilla* spp.), rely primarily on fibrous plant material that is highly abundant but low in energy, although they

also consume energy-rich fruits when seasonally available (Rothman et al., 2008). In contrast, much smaller primates, like callitrichids (*Callitrichidae* spp.), pursue protein- and energy-rich foods such as insects and gum, in addition to fruit and other plant parts (van Holstein et al., 2024). Body size determines not only the amount of energy required for daily activities (Gaulin, 1979) but also influences dietary choices, *foraging strategies*, and habitat selection (French & Smith, 2005; Jungers, 2013; Pontzer, 2015). Additionally, primates must balance their diets not just in terms of total energy intake but also by achieving species-specific nutritional goals (Raubenheimer et al., 2015). Coexisting species often exhibit differences in diets that are significant enough to reduce the effects of interspecific competition. Even among coexisting specialists, small differences in dentition result in notable differences in the plant species exploited, demonstrating that minute dietary specializations might be evolved adaptations to severe competition (Smith, 2010; van Holstein et al., 2024). This body size-mediated disparity in energy needs influences not only the amount of resources different species require but also how these species acquire resources and the types of environments they can inhabit (Brown et al., 2004).

Primate communities are characterized by complex interspecific interactions, particularly because many primates consume similar resources (Hladik, 1981). The overlap in dietary needs often results in intense competition for food resources, which plays an important role in shaping these communities. For instance, the presence of larger, more dominant species can limit the availability of resources for smaller, subordinate primates, forcing them to adjust their foraging strategies or shift their niche to avoid direct competition. *Bottom-up* factors, such as the availability of food and other resources, and *top-down* factors, such as the presence of predators, also contribute to the organization of primate communities. These

dynamics underscore the importance of understanding the ecological niche as a multidimensional concept with various biotic and abiotic facets, and in the case of primates, how these factors influence social behavior, reproductive strategies, and fitness.

1.3 PRIMATE FEEDING GUILDS

Feeding competition is considered a key mechanism that explains global patterns of diversity (Hutchinson 1959; Roughgarden 1983). It is a common and pervasive constraint that most primates face (Schrier et al., 2009), making the study of competition crucial to understanding their ecology, behavior, and physiology, especially where overlapping and similar-sized species coexist. It also serves to inform us about the evolutionary processes that governed the diversification of this extensive lineage and modern patterns of primate biogeography (Connell, 1980) and can help with the management and conservation of endangered species (Reed & Bidner, 2004). Competition among primates most commonly revolves around access to essential food resources, and it has a bidirectional relationship with a species' niche. The factors that define a species' ecological niche, such as diet, habitat preferences, and foraging strategies, inherently influence its competitive interactions with other species (Barabás et al., 2016; Costa-Pereira et al., 2019; Kamilar & Ledogar, 2011). These competitive interactions, in turn, can drive further adaptations and niche differentiation as species adjust their behavior, resource use, and even physiological traits to mitigate competition. Over time, this dynamic interplay continuously reshapes the niche of each species, reinforcing or altering its role within the ecosystem.

1.3.1 Combating the Effects of Competition

Animals employ various strategies to reduce interspecific resource competition and enhance coexistence in tropical environments. Many primates coexist with several other species of similar body size, resulting in similar energetic and nutritional needs (Fleagle et al., 1999; Lambert & Rothman, 2015). The set of species that exploit the same resources–i.e., feeding guilds– likely impose the strongest costs on each other (Simberloff & Dayan, 1991).

Natural selection drives competing species to shift their patterns of resource use to reduce the costs of competition among species with otherwise overlapping diets, a process known as *niche partitioning* (MacArthur, 1958). Such adaptations typically include changes in an animal's ecology, behavior, or physiology. Some species might specialize in slightly different diets or forage at different times (*temporal partitioning*) to reduce the potential for costly altercations (Terborgh & van Schaik, 1987; Ganzhorn, 1999). Some species occupy different areas, such as the edge of a habitat or different areas within the forest canopy, which might offer different ecological pressures than its core (Harris, 1988), enabling species to exploit distinct niches within the same habitat, further reducing direct competition (Schreier et al., 2009).

Primates in diverse communities often experience size-dependent hierarchies that determine the priority of resource access (Houle et al., 2010; Kamilar & Ledogar, 2011). A common, size-based form of ecological niche partitioning relies on the vertical stratification of rainforests, whereby species use different canopy levels (Almeida-Silva et al., 2005; Gautier-Hion et al., 1983; Houle et al., 2014; Thiel et al., 2021) as a means of niche partitioning (Schreier et al., 2009). Vertical stratification is the primary form of *spatial partitioning* in primate communities in African and Asian forests (Schreier et al., 2009), but it

is a global pattern observed in other primate and non-primate communities alike (Dutoit, 1990; Thiel et al., 2021; Vieira & Monteiro-Filho, 2003). This spatial division of feeding patches reduces competition among species that otherwise consume the same resources, and it is often governed by body size. For example, in Brazilian Atlantic forests, four competing neotropical primates exhibit size-based niche differentiation, with a positive relationship between body size and height of feeding strata; the largest of the species, the northern muriqui (*Brachyteles hypoxanthus*), forages in the highest strata–the emergent canopy; southern brown howler monkeys (*Alouatta guariba*), intermediate in size, in the canopy; the smaller black capuchins (*Sapajus nigritus*) occupy the understory and lower canopy; members of the smallest species, the buffy-headed marmoset (*Callithrix flaviceps*), were rarely observed, but anecdotal observations indicate that they prefer highly-disturbed areas along the forest edge, which the other species avoid (Almeida-Silva et al., 2005). This observation is largely consistent with other neotropical primate feeding guilds (Fleagle, 1984; Mittermeier & van Roosmalen, 1981; Peres, 1993; Terborgh, 2014a). Similarly, an East African frugivorous feeding guild composed of chimpanzees (*Pan troglodytes*), grey-cheeked mangabeys (*Lophocebus albigena*), blue monkeys (*Cercopithecus mitis*), and red-tailed monkeys (*C. ascanius*), also experiences a strong size-based hierarchy in which priority of access is dependent on body size; while each species tends to feed in tree crowns independently, dominant species easily monopolize prime, upper canopy feeding patches, evicting smaller ones to lower strata (Houle et al., 2010). These observations are consistent with the closed concept of communities, whereby interactions dictate community structure.

Another strategy by which primates reduce competition is the use of different *fallback foods*. These are abundant, lower-quality resources that primates rely on during periods of low

availability of their preferred, higher-quality foods (Marshall et al., 2009). These types of foods strongly shape dietary niche partitioning. They are relied upon during periods of environmental stress such as dry seasons or fruit shortages (Marshall & Wrangham, 2007), and they can reduce competition by providing alternative resources when species are excluded from accessing high quality items. However, fallback foods can also increase competition if they are limited or difficult to exploit (Marshall et al., 2009). For instance, in fruit-eating specialists, like chimpanzees and gibbons, fallback foods often consist of less-nutritious but more reliably available resources, such as figs and fibrous plant materials (Elder, 2009; Lambert & Rothman, 2015). Fruit availability strongly influences their activity patterns. Significant aggressive interactions may occur in fruiting trees, and species-specific preferences for certain fruits play a key role in reducing direct competition, especially during periods of scarcity (Stevenson et al., 2000). This dietary flexibility allows different species to coexist by reducing direct competition for the same high-value food resources during scarcity periods (Marshall et al., 2009). However, when essential fallback foods are scarce or nutritionally insufficient, competition can intensify, particularly if multiple species are forced to rely on the same limited resources (Wrangham et al., 1998). So, while fallback foods can mitigate competitive pressures, they can also exacerbate them, depending on their availability and the ecological context (Marshall & Wrangham, 2007; Lambert & Rothman, 2015). Therefore, dietary niche partitioning often manifests more in divergence in fallback food use rather than in preferred foods, as species adapt to exploit different resources to survive (Marshall et al., 2009). This divergence in fallback food usage is key to allowing multiple primate species within the same feeding guild to coexist, as it minimizes competition and facilitates niche differentiation (Marshall et al., 2009).

1.3.2 Polyspecific Associations

Interestingly, strong environmental constraints can also facilitate associations between competing species. Polyspecific associations, or mixed-species groups, are common in herbivores, including primates, and are primarily observed as a strategy to reduce mortality risk in environments where predation pressure is high (Burkepile & Hay, 2008; Pays et al., 2014; Prins & Douglas-Hamilton, 1990; Struhsaker, 1981; Waser, 1982). Among other benefits, such as increases in foraging efficiency, insect predation, and social opportunities (Buchanan-Smith, 1990; Gautier-Hion et al., 1983; Korstjens & Noë, 2004; Waser, 1982), these associations allow vulnerable species to benefit from increased vigilance and predator detection (Bryer et al., 2013; Chapman & Chapman, 2000; Gautier-Hion et al., 1983). These associations are especially common in dense forests and areas with a high density of predators, where the species involved often have complementary foraging habits, such as different feeding heights or dietary preferences, which reduce direct competition.

In primates, polyspecific associations can also be a natural setting to study interspecific competition. While these associations decrease predation risk through mechanisms like the dilution effect and enhanced predator detection (Hamilton, 1971; Kenward, 1978; Bshary & Noë, 1997a), they also introduce costs, particularly increased competition for resources with overlapping ecological niches. The balance between costs and benefits in these associations is influenced by different factors, such as the degree of dietary overlap between the species and the seasonal availability of food resources. When dietary overlap is low, species gain predator protection without significant competition; however, when overlap is high, as seen in some primate communities, competition for food can intensify, especially during periods of scarcity (Carlson et al., 2023; Chapman & Chapman, 2000). For example, Diana monkeys

(*C. diana*), which often form such associations with other guenons (*Cercopithecus* spp.), show increased daily travel when associated with heterospecifics, which might indicate increased foraging effort as a result of a decrease in food intake (Shultz, 2003). These associations are particularly noted in Africa and South America, where they likely evolved partly in response to predation risks from large eagles like the crowned eagle (*Stephanoaetus coronatus*) in Africa and the harpy eagle (*Harpia harpyja*) in South America (Terborgh, 1990).

In polyspecific associations, certain species, like grey-cheeked mangabeys, often serve as the protective species, offering antipredator benefits to others due to their effective predator detection and conspicuous behavior (Bryer et al., 2013; Bshary & Noe, 1997; Eckardt & Zuberbühler, 2004; Freed, 2006). However, the resulting competition can lead to competitive exclusion of the inferior species from certain forest strata or access to key resources (Buzzard, 2004; Eckardt & Zuberbühler, 2004). The dynamics of these associations are influenced not only by the presence of predators but also by patterns of food availability and the unique ecological niches of the species involved, highlighting the complexities of coexistence among competing species.

1.3.3 Intraguild Predation

The movement and distribution patterns of animals in a habitat are shaped by a complex interplay between foraging decisions (aka the "landscape of energy"; Gallagher et al., 2017) and predation risk (aka the "landscape of fear"; Laundré et al., 2010). Navigation involves a continuous decision-making process where animals weigh the costs of energy expenditure against the risk of encountering predators (Gallagher et al., 2017). These costs of movement are not uniform; they vary based on environmental features, such as terrain slopes or canopy

structures, which can significantly increase energy demands (McGrosky & Pontzer, 2023). To minimize predation risk, animals may alter their behavior and movement patterns, even at the cost of accessing fewer resources or expending more energy. Integrating these landscapes offers a comprehensive understanding of how animals distribute themselves across space and time (Gallagher et al., 2017).

An ecological puzzle arises when species that compete for the same resources, and are therefore attracted to the same productive areas, also engage in predator-prey interactions, known as intraguild predation (Amarasekare, 2008). Traditional models suggest that intraguild prey, typically the inferior competitors, should be excluded from resource-rich environments due to the combined pressures of competition and predation (Holt & Polis, 1997). However, empirical evidence often contradicts this, showing that intraguild prey can persist even in highly productive environments (Yu et al., 1990, Diehl 1992, Morin 1999; Diehl & Feissel, 2000, 2001). A notable example of this interaction exists among the frugivore guild at the Ngogo Research Station in Uganda. Chimpanzees, which are fruit specialists, have decimated the population of their preferred prey, the folivorous red colobus (*Procolobus rufomitratus*; Teelen, 2007; Watts & Amsler, 2013). As a result, chimpanzees have increased their predation on other species, including members of their feeding guild– the frugivorous red-tailed monkeys (McLester, 2020; Watts & Mitani, 2002). These interactions impose dual costs on the red-tails: they not only face the threat of predation, but they also lose access to high-quality fruits. When chimpanzees forage within their *home range*, red-tails either remain motionless for extended periods while the chimpanzees deplete resources or flee to less productive areas. Either response should result in reduced foraging efficiency and

energy intake; however, this has yet to be tested (but see Chapter 2). Despite these pressures, red-tails continue to thrive in this habitat (Frogge et al., 2022).

One explanation for the persistence of red-tails is the existence of mechanisms that provide intraguild prey with temporal or spatial refuges, allowing them to escape predation at critical times. These refuges might arise from differences in species' sensitivities to environmental factors, enabling prey to exploit conditions unfavorable to the predator (Amarasekare, 2000, 2008). In some systems, intraspecific interference among predators, such as cannibalism, can reduce their effectiveness, thereby allowing prey to persist (Polis et al., 1989). Infanticide and cannibalism are common in the Ngogo chimpanzee community (Watts & Mitani, 2000, 2002), and boundary areas between communities are less frequented by chimpanzees because of the risk of aggressive and violent altercations between chimpanzee communities (Mitani & Watts, 2001; Muller, 2002; Brown, unpub. census data). Such areas might offer relief through release from competition and predation for smaller frugivores, like red-tails.

A different explanation of such coexistence hinges on the competitive abilities of the prey; the intraguild prey must be a superior competitor for shared resources (Holt & Polis, 1997). It is unlikely that red-tailed monkeys are superior in their interference capabilities– i.e., their ability to win physical contests against chimpanzees. The Ngogo frugivore guild observes a strong, size-based hierarchy in competitive ability, and red-tails are the smallest-bodied species (Houle, 1997). However, red-tails find and exploit resources more rapidly, before larger competitors arrive and displace them (Waser & Case, 1981). This dynamic might facilitate the coexistence of intraguild predation in this system. In productive environments, strong intraguild predation can destabilize coexistence, with the potential for

exclusion of the prey species. While the red-tail population at Ngogo is seemingly growing (Frogge et al., 2022), chimpanzees have only relatively recently–within the last 20 years or so– increased their predation on red-tails (Watts & Mitani, 2002). Given the slow life history of red-tails (Cords, 1984; Cords & Sarmiento, 2013), it is possible that the effect of this predation is still unobservable and that red-tails might soon experience competitive and predatory pressures strong enough to begin limiting their population growth (e.g., Owen-Smith & Mills, 2008). Understanding the balance between competition and predation in guilds similar to the one at Ngogo is crucial for predicting species coexistence and community structure, particularly in productive environments like tropical rainforests, where these interactions are most pronounced.

1.3.4 Food as a Blessing or a Curse

Environmental factors play a significant role in shaping the nature and intensity of interspecific competition. The effect that food abundance has on competitive dynamics is particularly evident in species that rely heavily on ephemeral, limited, or highly seasonal food types, such as fruit (Isbell, 1991; Terborgh & Janson, 1986; van Schaik, 1989; Wrangham, 1980). The availability and distribution of food sources plays a fundamental role in determining within-species competition in primates (e.g., Isbell & Young, 2002; Janson & van Schaik, 1988; van Schaik, 1989; Wrangham, 1980), and yet, little is known about how it affects the interspecific interactions among members of a competitive guild. The effect of food availability on the direction and intensity of competition may vary. One straightforward possibility is that resource competition should intensify during periods of food scarcity, as limited availability forces species to compete more directly for essential resources (Peres, 1996). High resource abundance should reduce feeding competition by alleviating pressure

on limited resources, allowing for sustainable coexistence (Prejs & Prejs, 1987). A less expected outcome is that an abundance of resources could also strengthen competitive pressure because animals tend to have more overlapping diets when their preferred foods are plentiful, leading to more direct competition for the most desirable foods (Stevenson et al., 2000). In resource-scarce environments, species might partition their niches more distinctly, consuming different fallback foods and reducing direct competition (Marshall & Wrangham, 2007; Petersen et al., 2019; Prati et al., 2021; Stevenson et al., 2000; van Holstein et al., 2024). Even among folivores, whose food is ubiquitously abundant, competition exists over leaves with the highest nutrient content; when foods of high energy and nutritious quality are distributed in small patches, stronger or more motivated competitors can monopolize them, while weaker ones are forced to seek out less valuable resources (Sayers, 2013).

Is it possible, then, that a species would experience consistent competitive pressure during periods of both food abundance and scarcity? One key factor is the high overlap in dietary preferences with other species across seasons. In such cases, a species can experience intense competition during periods of high abundance as it and other species vie for the same high-quality resources (Stevenson et al., 2000). That species can also experience competition from the same or potentially other competitors during periods of scarcity as they compete for essential fallback foods (Marshall et al., 2009; Marshall & Wrangham, 2007).

In habitats where key resources are spatially limited or only available in small quantities, competition may remain high year-round. During periods of abundance, dominant species might monopolize these desirable resources, forcing others to settle for suboptimal options, and during scarcity, competition for any remaining resources becomes even fiercer. In highly

seasonal environments, where there is a sharp contrast between periods of abundance and scarcity, a species might confront different sets of competitors at different times of the year, leading to sustained competition throughout the year. Lastly, species with a narrow dietary niche or limited behavioral flexibility may struggle to adjust their feeding strategies in response to changes in resource availability, resulting in persistent competition for limited resources (van Holstein, et al., 2024; Schreier, et al., 2009). In such scenarios, these species are unable to escape the pressures of competition, whether resources are plentiful or scarce, leading to ongoing competitive challenges that shape their ecological niche and survival strategies.

While the two competitive conditions–i.e., over primary versus fallback foods–are not mutually exclusive, it is highly unlikely that a species can thrive while suffering from high competition when food is abundant and when it is scarce; such a situation should lead to prolonged energy deficits, resulting in limited reproduction, declining populations, and eventually local extinction.

1.3.5 Competition Across Scales

Individual-level behaviors, such as an animal's response to competition, predation, and the pressures of growth and reproduction, are fundamental drivers of population- and species-level patterns (Clutton-Brock & Sheldon, 2010; Wong & Candolin, 2015). These behaviors aggregate to form larger-scale ecological phenomena, but the manner in which they scale up can be complex and non-linear, often resulting in unexpected population-level outcomes. At the individual level, animals respond to selective pressures like competition and predation by altering their behavior, movement patterns, and energy allocation. An

animal facing high competition for food might reduce foraging in high-competition areas or shift to alternative resources (Seiler & Robbins, 2020), while an animal under threat from predators may adjust its habitat use to reduce exposure to risk (Lima & Dill, 1990). These decisions are crucial for survival and reproduction at the individual level and reflect the foundational behaviors that then shape ecological patterns at higher levels.

The dynamics of competition, whether within or between species, vary significantly. Intraspecific competition is typically more intense because individuals of the same species have nutritional and energetic requirements much more similar to each other than to those of other species. These similarities in demands lead to direct confrontations over food, territory, or mates, which can foster territoriality, dominance hierarchies, and resource monopolization (Isbell, 1991) and lead to varying social structures that characterize the species. Interspecific competition, on the other hand, is usually less direct, as species compete for overlapping but not identical resources, often leading to niche differentiation or spatial separation to avoid conflict (Connell, 1980). The intensity of competition can shift depending on resource availability and population density. At high population density, intraspecific competition escalates, leading to resource depletion, stress, and reduced reproductive success (Begon et al., 2006). This can push individuals to adopt riskier behaviors, such as venturing into predator-rich areas (Lima & Dill, 1990). However, individual behavior does not always translate into population-level dynamics in a direct or linear manner. For example, density-dependent competition may allow for coexistence at low densities, but at higher densities, competition escalates disproportionately, leading to population crashes (Begon et al., 2006). Similarly, predation thresholds can trigger abrupt population declines once predators surpass a critical number, overwhelming previously

effective avoidance strategies (Estes et al., 1998). While niche partitioning can stabilize interspecific competition, environmental changes may disrupt this balance, leading to cascading effects within ecosystems (Chesson, 2000).

Understanding the relative strength of intraspecific versus interspecific competition is crucial for predicting *population dynamics* and community structures. Intraspecific competition often proves stronger due to the shared resource needs within a species, driving direct competition for food, territory, and mates (Begon et al., 2006; Strier, 2011). However, interspecific competition can also exert significant pressure, especially in environments where resource overlap between species is high (Connell, 1980). In such cases, scarcity can trigger sudden population shifts as species compete within overlapping niches, potentially leading to competitive exclusion or coexistence depending on resource partitioning strategies (Chesson, 2000; Tilman, 1982). Both types of competition also interact with selective pressures like predation and reproductive demands, further complicating population outcomes. As population density increases, intraspecific competition typically intensifies, promoting stronger territorial or hierarchical systems (Isbell, 1991), while interspecific competition often leads to niche differentiation, enabling species to coexist and stabilizing community dynamics (Chesson, 2000; Holt et al., 1994).

Given these complexities, it is essential to incorporate both within- and between-species competition into ecological models to capture the full range of interactions that shape population and community dynamics. While individual behaviors are the building blocks of ecological interactions, the aggregation of these behaviors often produces emergent patterns that require a better understanding of non-linear processes, threshold effects, and the interaction of different types of competition (Stephens & Sutherland, 1999; Begon et al.,

2006). To effectively account for the impact of both intra- and interspecific interactions on a species, one approach is to model how environmental fluctuations or resource pulses shift the balance between these forms of competition. During periods of resource scarcity, intraspecific competition may intensify as individuals of the same species directly compete for dwindling fallback foods, while interspecific competition might diminish due to niche specialization among different species. Conversely, in times of abundance, species may converge on high-quality resources, amplifying interspecific competition. If we can accurately measure competition, we can capture these shifts across temporal or spatial scales (Tilman, 1982; Yang et al., 2008). These models would highlight how fluctuating resources modify the balance of competition, offering insights into how species interactions change under different environmental conditions.

Additionally, integrating the concept of facilitative interactions alongside competition can provide a more complete view of how species navigate their biotic environments. Facilitative interactions (e.g., intraguild polyspecific associations) may buffer the effects of intraspecific competition, even while interspecific competition persists (Brooker et al., 2008; Bruno et al., 2003). For example, red-tailed monkeys can only access Monodora, a large and fleshy fruit, when grey-cheeked mangabeys break through its thick shell first (Struhsaker, 1981). Mangabeys are also thought to flush insects while foraging, which red-tails consume opportunistically (Gautier-Hion et al., 1974). These interactions can benefit red-tail individuals by creating more foraging opportunities and reducing direct intraspecific competition (Brooker et al., 2008). Such opportunities are particularly important when resources are limiting and would otherwise be monopolized by dominant individuals within the species. Evaluating the relative strength of facilitation versus competition could reveal

complex dynamics that shape community structures, and combining these interactions into competition models offers a holistic view of species' responses to multiple concurrent food-web interactions across varying ecological contexts.

1.4 Energetic Effects of Competition

1.4.1 The Physiology of Being Small

As discussed above, the amount of energy an individual can access will depend on many environmental factors before the energy reaches and can be incorporated into an individual's body. Once consumed, the amount of energy available to expend will depend primarily on intrinsic physiological factors, like digestive capabilities, the efficiency of nutrient absorption and metabolism, and allocation priorities within the body (Pontzer, 2015). Total Energy Expenditure (TEE) in primates comprises the comprehensive energy costs associated with basal metabolic rate (BMR), physical activity, thermoregulation, growth, maintenance, and reproduction. BMR, which represents the minimum energy required for vital organ functions at rest, scales *allometrically* with body mass, meaning that smaller primates expend more energy per unit of body mass compared to larger animals (aka 'Kleiber's Law'; Kleiber, 1947). This demands that small-bodied primates maintain diets high in nutritional content and/or feed more frequently to meet their physiological needs (Sailer et al., 1985), particularly in competitive environments. Physical activity is a significant component of TEE, covering energy used for movement, foraging, and social interactions. Muscles at rest use minimal energy (Elia, 1992; Wang et al., 2011), but physical exertion allocates considerable energy to operate muscles, which can greatly increase energy expenditure above BMR. Despite their typically high levels of activity, small-bodied primates often exhibit a

lower-than-expected proportion of TEE dedicated to physical activity due to compensatory mechanisms such as efficiently reducing BMR during rest periods (Black et al., 1996; Elia et al., 2000).

Given their higher energy needs relative to body size, small-bodied primates are particularly vulnerable to fluctuations in food availability (Chapman et al., 2012). This vulnerability necessitates a selective diet, focusing on foods with the highest nutritional value and least foraging effort. Unsurprisingly, *ripe fruit*, an energy-rich type of food, is a staple in the diets of many primates (Chivers, 1980), even among many facultatively folivorous species (Chivers, 1998; Hladik, 1977; Rothman et al., 2008). In competitive environments, these primates may adopt specific foraging strategies to avoid direct competition with larger species, such as targeting different food resources or adjusting their feeding times. For example, red-tailed monkeys, like other cercopithecines, have evolved longer alimentary transit times, enhancing nutrient extraction from less nutrient-dense and sought-after food sources (Lambert, 1998). Conversely, one of their competitors, grey-cheeked mangabeys, employs robust dentition and mandibles to exploit hard alternative food sources, like bark or seeds, when preferred fruits are scarce (Lambert et al., 2004). Small primates are also spatially limited compared to larger species with expansive home ranges. To specialize in nutrient-dense but ephemeral foods like ripe fruit, a species needs to be able to cover large areas (like bats, birds, and chimps). Small-bodied primates cannot do this; no matter the habitat, they always have a much smaller range than larger species in their feeding guild (Harvey & Clutton-Brock, 1981). To cope with this spatial limitation, they must rely on a more diverse food base than the larger competitors, with more options within their home ranges.

Reproductive physiology in small-bodied primates is intricately linked to their energy budgets, particularly in environments where food scarcity is common. While male reproduction is less dependent on energy availability, female reproduction—especially gestation and lactation—requires significant energy investment (Emery Thompson, 2013; Key & Ross, 1999; Schneider, 2004). This necessitates careful energy allocation, with females facing significant trade-offs to ensure both their survival and successful rearing of offspring, making them highly susceptible to energetic stress (Thompson et al., 2010). Unlike other animals that can adjust litter sizes under caloric limitations, primates generally produce one dependent offspring at a time (Chapman, 1990), making reproductive success heavily reliant on stable energy access. Insufficient energy can lead to extended inter-birth intervals or decreased likelihood of conception, with competitive pressures further limiting access to essential resources (Ellison, 2003; Emery Thompson et al., 2012; Emery Thompson & Wrangham, 2008). Thus, in times of food scarcity, or if competitive pressure is high enough to prevent small-bodied primates from consuming sufficient energy, they may delay reproduction or reduce investment in offspring, balancing energy conservation with reproductive success. By increasing energetic stress, through which female reproduction might suffer, interspecific competition has the potential to limit both life-long fitness in individuals as well as population growth. These physiological adaptations underscore the profound impact of environmental pressures on the survival of small-bodied primates. The complex interplay between their physiological needs and *ecological constraints* highlights how energy limitations shape not only individual fitness but also broader patterns of species interactions and ecosystem dynamics.

1.4.2 Metabolic Theory vs. Dynamic Energy Budget

Animals live by two primary drivers: the need to find food and the ability to convert that food into offspring, thereby maximizing their fitness. Metabolism is the pathway through which energy is transferred between these stages. It is a set of chemical reactions that are necessary for life, and it converts energy and nutrients into fuel and other building blocks necessary for cellular processes.

Optimal Foraging Theory (Charnov 1976; Sih and Christensen 2001) suggests that a forager's diet is influenced by environmental factors–like food nutritional quality, handling times, and distribution–as well as the forager's physiological traits. An animal's optimal diet is determined by the profitability and availability of different foods, with diets narrowing when high-quality foods are abundant and expanding to include less profitable items when they are scarce (Pyke et al., 1977). Thus, dietary niche breadth (Shipley et al., 2009) is shaped by the animal's anatomy and physiology and the environmental conditions it faces. The variation in body size within ecological feeding guilds introduces additional layers of complexity, as species with different sizes often compete for the same resources but have differing energetic needs. Smaller species, with their higher metabolic rates and greater surface area-to-volume ratios, must consume proportionally more energy-rich and nutritionally dense foods to meet their physiological demands (Sailer et al., 1985). This divergence in energetic requirements, despite overlapping diets, can lead to distinct foraging strategies and resource use patterns among otherwise similar ecological niches.

The *Metabolic Theory of Ecology* and *Dynamic Energy Budget* offer broad frameworks for understanding how energy influences ecological processes. The Metabolic Theory of Ecology proposes that the metabolic rate of organisms drives their ecological dynamics,

scaling predictably with body size and temperature (Brown et al., 2004). This theory suggests that small primates, with their larger surface area-to-volume ratios, face heightened physiological demands, requiring them to consume more energy relative to their body size compared to larger animals (Gaulin, 1979; Kleiber, 1947). As a result, small-bodied primates are more sensitive to fluctuations in food availability and the intensity of competition. The Dynamic Energy Budget, on the other hand, focus on how organisms allocate energy throughout the life cycle, balancing energy intake with the demands of growth, maintenance, and reproduction (Kooijman et al., 2004). This theory underscores the importance of efficient management of energy resources, particularly for small-bodied primates whose access to high-quality foods is strongly influenced by competition from larger species.

The Metabolic Theory of Ecology emphasizes the constraints imposed by metabolic rate on the ecological roles and energy needs of small primates, potentially driving them to exploit different ecological niches or strata within forests to reduce competition with larger primates (Brown et al., 2004; Gaulin, 1979). The Dynamic Energy Budget provides a complementary perspective by explaining how these primates allocate their limited energy resources across various physiological processes, offering insight into the adaptive strategies that enable them to survive and reproduce despite competitive pressures, such as optimizing energy use and diversifying their foraging strategies (Kooijman et al., 2004; Emery Thompson et al., 2012). These frameworks provide valuable insights into how small-bodied primates navigate the energetic challenges of resource competition and survival. The Metabolic Theory of Ecology posits that the high metabolic rates of small primates necessitate frequent access to high-quality food, compelling them to either efficiently exploit available resources or adapt their foraging strategies when larger competitors dominate

preferred food sources. The Dynamic Energy Budget complements this by elucidating how these primates allocate their limited energy resources toward essential physiological processes under competitive pressures. For instance, tamarins and marmosets may reduce competition with larger primates by specializing in insects and tree exudates (Metabolic Theory of Ecology) while also adopting energy-efficient territorial behaviors (Dynamic Energy Budget) to optimize resource use (Miller et al., 2006; Rylands & de Faria, 1993; van Holstein et al., 2024).

Habitat use and partitioning further illustrate how small-bodied primates mitigate competition and ensure resource availability. According to the Metabolic Theory of Ecology, these primates often occupy different ecological niches or vertical strata within forests to reduce direct competition with larger species, allowing them to access less-exploited resources and optimize energy intake. The Dynamic Energy Budget theory expands on this by explaining the balance small primates must strike between energy allocation for foraging and other physiological needs. However, both the Metabolic Theory of Ecology and Dynamic Energy Budget have limitations in predicting species interactions within ecological communities, as they do not fully account for variations within species, short-term fluctuations in energy demands, or how different species within a guild might interact under varying competitive pressures and food availability. Integrating insights from both the Metabolic Theory of Ecology and the Dynamic Energy Budget is essential to understanding the complex dynamics of primate communities, particularly the interspecific competition experienced among small-bodied primates. The Dynamic Energy Budget provides a detailed framework for energy allocation within individual primates. Still, it falls short in predicting how these allocations are affected by interactions with other species, especially in fluctuating

environments (Kooijman et al., 2004). The Metabolic Theory of Ecology offers a broader perspective on how metabolic rates influence ecological interactions across species. Yet, it overlooks finer-scale, intra-species variations and real-world complexities in *energy balance* and competition (Brown et al., 2004). Focused research is needed to bridge these gaps by exploring the energetic and reproductive costs of interspecific competition among small primates in both stable and fluctuating environments.

Despite the well-documented impact of intraspecific competition on access to food and reproductive success in primates (Isbell, 1991; Janson & van Schaik, 1988; Koenig, 2002, 2002; Majolo et al., 2012; Sterck et al., 1997; van Schaik, 1989), there remains a significant gap in our understanding of how interspecific feeding competition shapes these outcomes, and the energetic costs and reproductive consequences of competition with other species have not been systematically investigated. This oversight is particularly surprising given the evidence that such competition likely plays a crucial role in shaping community dynamics (Connell, 1983; Fleagle et al., 1999), particularly in diverse primate guilds where species with overlapping diets coexist. The lack of research on this topic leaves a critical void in our knowledge of how interspecific interactions influence the fitness and survival of sympatric primates. As primate communities face new challenges like habitat degradation and climate change, understanding these historical influences becomes increasingly important for predicting future changes and informing conservation strategies (Chapman et al., 2012). Studying extant primate communities offers insights not only into how evolutionary histories, habitats, and species interactions shape biogeography but also into how modern impacts might reshape or even reconstruct future communities. Such knowledge is crucial for effective species management and conservation efforts (Estrada et al., 2017).

Understanding the effects of interspecific competition is essential, as it can alter energy intake and allocation, reproductive timing, and social interactions in ways that differ significantly from intraspecific dynamics (Goldberg & Barton, 1992). For example, lapwings and golden plovers primarily experience intraspecific competition for food when they co-occur in mixed-species flocks, except when gulls are present (Barnard & Stephens, 1981; Barnard et al., 1982). The addition of gulls, an aggressive kleptoparasitic species, intensifies interspecific competition, significantly reducing lapwing foraging efficiency and energy intake by altering their prey selection behavior. The absence of such empirical data on the energetic costs of interspecific competition is a major limitation in current primate ecological models, which often overlook or underestimate the role of these interactions.

1.5 Measuring Competition

Understanding and measuring competition presents significant challenges, yet it is crucial, especially in primates, as most species live among multiple competitors (Schrier et al., 2009), and the effects of these interactions among them are poorly understood. Competition can be challenging to observe because it is not always direct; for example, many primates exhibit evolved behaviors that reduce direct conflict (Connell, 1980), which are adaptations to conflicts in the species' coevolutionary history. While this makes competition less visible to human observers, it does not eliminate its presence. Furthermore, primates experience competition at multiple scales—between individuals, among groups, and between species—all of which must be considered when estimating the ecological environments they inhabit.

Given the difficulties in direct observation, a better approach might be to measure the outcomes of competition. For instance, primates often compete for access to food, so

discrepancies in food intake can indicate differences in competitive abilities (Bergstrom et al., 2020; Brown et al., 2022). This approach, however, also presents challenges. Primates exhibit flexible and diverse diets (Chapman et al., 2002), and accurately measuring consumption across different environments and time scales is labor-intensive and costly. Additionally, the nutrient content of fruits, a major dietary component for most primates, varies significantly between species and even within individual plants (Houle et al., 2014), complicating estimates of the amount of energy and nutrients that primates consume. Phenological studies, which track food availability through counts or biomass, offer another avenue but can be inaccurate and labor-intensive, and are prohibitively expensive for long-term studies (Chivers, 1998).

To overcome these challenges, it is essential to develop more inclusive research designs that simultaneously consider multiple factors, including interspecific competition and other food-web interactions, and food availability. Instead of focusing on a single biotic interaction in studies of wild primates, incorporating multiple ecological interactions can more accurately capture the complexity of ecological interactions. For example, resource availability interacts with different hunting modes of predators to shape ecosystems (Schmitz, 2008), highlighting the need for these multifaceted designs. By expanding research frameworks to account for these variables as they relate to primate guilds, we can better understand how competition interacts with food availability and other interactions to influence both individual behaviors and broader community structures.

Another issue lies in the difficulty of distinguishing between intraspecific and interspecific competition, especially when environmental variability obscures these effects. Most primate studies have historically focused on the social and fitness consequences of

intraspecific competition (Isbell, 1991; Sterck et al., 1997; Terborgh & Janson, 1986; van Schaik, 1989; Wrangham, 1980), often overlooking the outcomes of interspecific interactions. Combining these scales into a singular model could help us better understand these competitive dynamics when they overlap. For example, when population density is high, intraspecific competition tends to intensify, leading to resource depletion and elevated stress (Begon et al., 2006). At the same time, individuals may adopt riskier strategies, such as feeding in predator-rich areas. Additionally, short-term studies may miss important temporal and spatial fluctuations that shape population dynamics and competition, leading to incomplete or misleading conclusions (Pimm & Redfearn, 1988). This underscores the importance of expanding studies to consider long-term fluctuations and interspecies dynamics, as increasing the temporal and spatial scope of studies can reveal critical insights.

Finally, the intricate nature of competition, combined with indirect facilitative interactions, adds another layer of complexity. Positive interactions between species, such as facilitation, can buffer the effects of competition by altering resource availability or reducing the stress of direct confrontation (Brooker et al., 2008). To address this, integrating advanced modeling approaches allows researchers to simulate complex interactions and predict outcomes under various ecological scenarios. Chesson (2000) offers a framework for understanding species diversity in competitive environments, demonstrating how species can coexist by exploiting different conditions. Similarly, Gurevitch et al., (2000) show how competition and predation can interact, either reducing or exacerbating competitive pressures.

By pursuing these avenues—developing sophisticated study designs, expanding the temporal and spatial scope of studies, and integrating advanced modeling approaches—

researchers can improve their ability to measure and understand the complex dynamics of competition in primate and ecological communities.

1.5.1 Roadmap

This dissertation introduces new perspectives within the field of primate feeding ecology to investigate the costs of interspecific competition among primates in a tropical rainforest environment. Interspecific competition is notoriously difficult to quantify, leaving significant gaps in our understanding of its physiological consequences, especially in small-bodied primates, which are more susceptible to its outcomes. In response to these challenges, I examine the impact of feeding competition on the energy dynamics and physical condition of red-tailed monkeys in Kibale National Park, Uganda, using novel approaches including the use of biomarkers of energy gain and remote-sensed vegetation indices to predict primate foraging behavior. The research presents new insights into how primates navigate different types of competitive pressures in their environment and offers new approaches for studying primate energetics in complex ecosystems.

First, I address the matter of quantifying competition. In Chapter 2, I measure the energetic consequences of interspecific competition on smaller-bodied red-tailed monkeys, from larger-bodied intraguild predators, chimpanzees, along with competitors that facilitate protection from aerial predators. To measure net energy gain, I employed a novel approach using urine samples that were collected opportunistically and non-invasively, and analyzed for *C-peptide*, a biomarker of energy balance, across six social groups of red-tailed monkeys. This chapter explores how the presence of chimpanzees and other competitors affects the energy balance of red-tailed monkeys. Using a variety of data types to explore the biological

interactions that red-tails experience, I constructed linear mixed-effect models to examine the interaction between food availability, foraging, and the resulting energy balance, with respect to the presence of several competitors. This approach demonstrated that traditional methods of measuring food availability may not adequately capture the realized niche of a subordinate species in the *competitive hierarchy*. This chapter highlights the profound role of interspecific competition in shaping primate foraging behavior and energy dynamics, providing critical evidence for integrating interspecific competition into predictive models of primate behavior.

Measuring food availability in tropical forests is particularly challenging due to the variability of nutrient content in primates' food sources. Traditional phenological methods, while useful, are time-intensive and limited in spatial and temporal resolution. In Chapter 3, I shift the focus to an alternative measure of habitat productivity– remote-sensed vegetation indices–as predictors of primate foraging behavior. This chapter explores the utility of the Enhanced Vegetation Index (EVI) as a more objective and scalable tool for assessing food availability. EVI has thus far been used in studies of many other taxa, but in primates, only for leaf-eating species, or fruit-eating ones in dry and open habitats. I combined four years of EVI data with phenological surveys and urinary C-peptide measurements from the same red-tail social groups as in Chapter 2 to test whether EVI could serve as a reliable predictor of food availability and primate energy gain. The chapter presents a detailed analysis of how EVI, measured at different temporal lags, correlates with primate energy gain, highlighting the potential for remote-sensing technologies to revolutionize habitat monitoring and conservation efforts for frugivorous primates.

Finally, in Chapter 4, I examine the long-term energetic costs of competition by investigating the relationship between competition intensity and the physical condition and reproduction of red-tailed monkeys. This chapter introduces a metabolic biomarker panel designed to provide a comprehensive view of energy mobilization: energy balance, muscle mass, metabolic rate, ketosis, and protein catabolism. By analyzing non-invasive urine and fecal samples collected from nine groups of red-tailed monkeys, I conducted a clustering analysis combined with a threshold-based decision-tree approach to identify distinct metabolic profiles across groups facing varying levels of competition. The results revealed how groups experiencing high competition exhibited more severe energy deficits, suggesting prolonged periods of food stress, but that this did not manifest in differences in reproductive outcomes. This chapter provides critical insights into how interspecific competition affects not only immediate foraging success but also long-term physical condition, with implications for reproductive success and population growth.

These chapters offer new and exciting approaches to studying the costs of interspecific competition in red-tailed monkeys at varying biotic levels: the physical environment in which they live, the ecological interactions within their feeding guild, and their intrinsic physiological mobilization of energy under varying competitive conditions. By addressing the gaps in how we measure food availability and competition, this dissertation advances our understanding of primate feeding ecology and provides important tools for conservation and management in rapidly changing ecosystems.

1.6 DEFINITIONS

Key terms and definitions: a list of terminology used throughout the dissertation.

1.6.1 Ecology

Feeding Guild: A group of species that exploit the same class of environmental resources in a similar way, often leading to competition. (Simberloff & Dayan, 1991)

Interspecific Competition: Competition between different species for the same resources, such as food or habitat. (Connell, 1983)

Trophic Levels: The hierarchical levels in an ecosystem, comprising producers at the base and apex predators at the top. (Lindeman, 1942)

Ecological Niche: The role and position a species has in its environment, including all its interactions with the biotic and abiotic factors. (Hutchinson, 1957)

Niche Partitioning: The process by which competing species use the environment differently to coexist. (Schoener, 1974)

Exploitation Competition: A form of competition where all individuals have equal access to resources, leading to a "first come, first served" scenario. (Putman, 1996)

Interference Competition: A form of competition where access to resources is determined by dominance, aggression, or territorial behavior. (Putman, 1996)

Resource Partitioning: The division of resources by species to avoid direct competition. (Pianka, 1974)

Spatial Partitioning: The division of space among species to reduce competition. (Schoener, 1974)

Temporal Partitioning: The division of time among species to reduce competition, such as feeding at different times of day. (Schoener, 1974)

Top-Down Control: Ecological regulation by predators or higher trophic levels that control the abundance of and distribution of lower trophic levels. (Hairston et al., 1960)

Bottom-Up Control: Ecological regulation by the availability of resources at lower trophic levels that control the abundance and distribution of their consumers in higher trophic levels. (Hairston et al., 1960)

Primary Productivity: The rate at which energy is converted by photosynthetic organisms to organic substances. (Odum, 1959)

Abiotic Factors: Non-living chemical and physical parts of the environment that affect living organisms and the functioning of ecosystems. (Odum, 1959)

Biotic Interactions: Interactions between living organisms in an ecosystem, including competition, predation, and mutualism. (Odum, 1959)

Population Dynamics: The patterns and processes of change in populations over time, including growth rates, survival, and reproduction. (Hutchinson, 1978)

Speciose Communities: Communities that contain a large number of different species. (Emmons, 1999)

Competitive Exclusion: The principle stating that two species competing for the same limiting resources cannot coexist at constant population values. (Gause, 1934)

Food Web: A complex network of feeding relationships between organisms in an ecosystem. (Elton, 1927)

Competitive Hierarchies: The structured order of dominance and access to resources among species or individuals within a community. (Houle et al., 2010)

1.6.2 Primate Ecology and Behavior

Polyspecific Associations: Associations between two or more species that provide mutual benefits, such as predator avoidance. (Waser, 1982)

Home Range: The area in which an animal lives and moves on a periodic basis. (Harvey & Clutton-Brock, 1981)

Ranging Behavior: The spatial movements and territorial behaviors of animals within their home ranges. (Clutton-Brock, 2012)

Predation Risk: The potential likelihood of an organism being preyed upon in its environment. (Lima & Dill, 1990)

Vertical Stratification: The vertical layering of a habitat or ecosystem, often leading to niche partitioning among species. (Richards, 1971)

Foraging Strategies: The set of behaviors and tactics used by animals to locate, obtain, and consume food. (Stephens & Krebs, 1986)

Fallback Foods: Alternative food resources that animals rely on when preferred foods are scarce. (Lambert & Rothman, 2015)

Nutritional Landscape: The spatial and temporal distribution of food resources in an environment. (Raubenheimer et al., 2009)

Size-Based Hierarchy: A competitive structure where larger individuals or species dominate over smaller ones in access to resources. (Houle et al., 2010)

Fruit-Based Diets: Diets that are predominantly composed of fruits, which are often high in sugars and other nutrients. (Wrangham, 1977)

Ripe Fruits: Fruits that have reached their full size and are ready to eat, often high in sugars and other nutrients. (Wrangham, 1977)

1.6.3 Physiology and Energetics

Energetic Cost: The amount of energy expended by an organism to perform activities such as foraging, mating, or avoiding predators. (Emery Thompson, 2017)

Energetic Suppression: A decrease in energy gain or efficiency due to environmental or competitive pressures. (Emery Thompson et al., 2012)

Energy Balance (E_B): The difference between energy intake through food and energy expenditure by an organism. (Emery Thompson & Knott, 2008)

Basal Metabolic Rate (BMR): The rate at which an organism expends energy to maintain basic physiological functions at rest. (Kleiber, 1947)

Metabolic Theory of Ecology (MTE): A theory that describes how metabolic rate influences ecological dynamics, scaling predictably with body size and temperature. (Brown et al., 2004)

Dynamic Energy Budgets (DEB): A theoretical framework that explains how organisms allocate energy throughout their life cycle for maintenance, growth, and reproduction. (Kooijman et al., 2004)

Allometric Scaling: The study of the relationship between the size of an organism and its shape, anatomy, physiology, and behavior. (Kleiber, 1947)

C-Peptide: A by-product of insulin production that can be used as a biomarker for energy balance in humans and non-humans primates. (Sherry & Ellison, 2007)

Thermoregulation: The process by which animals maintain their body temperature within certain boundaries, even when the surrounding temperature is very different. (Scholander et al., 1950)

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II. Quantifying Interspecific Competition: Energy Consequences of Intraguild Feeding Competition in a Primate Community

2.1 MAIN

Interspecific competition for food is a fundamental constraint influencing reproduction (Yunger et al., 2002), social interactions (Carrete et al., 2010), as well as community structure and stability (Kamilar & Ledogar, 2011). Competitive dynamics are affected by species-specific traits like body size, abundance, and extrinsic mortality risk (Chase et al., 2002; Houle et al., 2010), and differences in physical capabilities can lead to asymmetric competitive outcomes (Law et al., 1997). However, models describing the ecological determinants of social (Dunbar, 1996; Janson & Goldsmith, 1995; Sterck et al., 1997; Terborgh & Janson, 1986; Wrangham, 1980) and biological (Clutton-Brock et al., 1977; Clutton-Brock & Harvey, 1977; Harvey & Clutton-Brock, 1985; van Schaik & Brockman, 2005) outcomes in primates often overlook the role of interspecific competition over resources. Some assume that it is insignificant relative to intraspecific competition and other ecological factors (Wrangham, 1980), or even overlook it entirely (Isbell & Young, 2002; Koenig, 2002). Nonetheless, the documented importance of interspecific competition in other taxa (Connell, 1983) highlights its potential to reshape our understanding of primate behavior and community interactions (Fleagle et al., 1999). Importantly, interspecific competition is not a static ecological factor. It is a highly dynamic force that can vary temporally and spatially (Schmitt & Holbrook, 1986; Thompson, 1988), and even seemingly weak competitive interactions can easily intensify to surpass those of intraspecific competition when common resources are depleted (Hu & Tessier, 1995). Given that

dominance relationships are observed between primates and other competitors (Houle, 1997; Stevenson et al., 2000), it is likely that interspecific competition exerts substantial pressures on primate populations, most of which reside in biodiverse environments and are members of *speciose feeding guilds* (Schreier et al., 2009). This perspective aligns with biogeographic patterns that show the influence of interspecific competition on species distributions and community structure (Dayan & Simberloff, 2005).

To date, studies of primate communities (e.g., Chapman et al., 2005; Falótico et al., 2021; Gautier-Hion, 1980; Houle et al., 2006; Struhsaker, 1978) have not measured how the strength or timing of interspecific feeding competition affects the energetic condition of sympatric species, nor its corresponding fitness outcomes. In reality, observations relating foraging behavior, energy gain, or reproduction in wild primates often diverge from model predictions (Clutton-Brock & Janson, 2012), indicating missing elements in the models. Examining how interspecific competition influences individual behavior can strengthen predictions about the mechanisms driving social and ecological interactions. Strong, size-based interspecific hierarchies can strengthen previously weak intraspecies hierarchies for access to food (Carrete et al., 2010; Thornton et al., 2015) and space (Forsman et al., 2007), leading to heightened aggressive and territorial behavior, and is expected to have downstream effects on individual health and reproduction. Here, we demonstrate that primate interspecific competition is highly variable in space and time and has substantial effects on patterns of energy gain in a small-bodied primate.

Sufficient energy intake is crucial for survival, growth, and reproduction (Emery Thompson, 2017; Emery Thompson et al., 2012). However, the impact of resource competition within primate feeding guilds (i.e., sympatric species that exploit the same resources) is poorly understood, particularly in terms of how it shapes the energetic

condition of species in competitor-dense environments (Chivers, 1998; Houle et al., 2006). First, accurately measuring the limiting resource, food – its abundance and distribution, its energetic and nutritional quality, and the degree of individual access to available resources – is essential yet prone to significant error (Morellato et al., 2018). This complexity arises from the diverse and flexible diets consumed by primates and the ephemeral nature of both the quantity and quality of foods in tropical rainforests (Houle et al., 2014) and because the decision to pursue particular foods is dependent on the food's frequency in the habitat (Davis et al., 2022; Greenwood, 1984), which should influence competitive interactions. More fundamentally, feeding competition is especially difficult to measure in natural settings, regardless of whether it is direct ('*interference competition*') or indirect ('*exploitation competition*'; Putman & Putman, 1994). Moreover, fully documenting the fitness outcomes associated with competitive pressure requires decades of data collection - because primates experience relatively slow life history pacing - on multiple social groups to identify its impacts on individual fitness and population dynamics. In lieu of a long-term study, we propose a more rapid method to track short-term changes in access to food energy as a means of studying interspecific feeding competition.

Within feeding guilds, larger animals often monopolize resources through intimidation or aggression, leaving smaller animals to rely on exhaustive search strategies within limited areas to quickly detect and either consume preferred resources before larger competitors arrive, or switch to less valuable foods (MacArthur, 1972; Waser & Case, 1981). This dynamic subjects both competitors to exploitation competition, but smaller species also experience interference from larger species. Consequently, while dominant species benefit directly from increases in food abundance (i.e., a positive relationship between food abundance and energy gain), the ability of a smaller or submissive consumer to access

available foods should be contingent upon the strength of competition from larger consumers. This study examines the impact of such dynamics on red-tailed monkeys (*Cercopithecus ascanius*; fe/male body weight = 2.8/3.7 kg, Cords et al., 2013), small-bodied, arboreal primates that consume many of the same foods as their largest competitor, eastern chimpanzees (*Pan troglodytes*; 34.4/41.7 kg, Emery Thompson & Wrangham, 2013; Fig. 2.1). Though ripe fruits appear to be a preferred food item for red-tails, they also commonly consume unripe fruits, flowers, leaves, and insects, as well as smaller amounts of fungus, pith, and other items (Bryer, 2020; Chapman et al., 2002; Struhsaker, 2017). Reproduction in red-tails does not correspond with patterns of fruit availability or nutrient intake (Rode et al., 2006), suggesting one or more intervening variables between the availability of food energy in the environment and individual energy income. In speciose communities with significant dietary overlap, interspecific competition might be a stronger limiting force on energy gain than food availability itself.

At the Ngogo research site in Kibale National Park, Uganda, the chimpanzee community occupied a much larger home range (~35 km^2, circa 2012; Fig. 2.2a; Mitani et al., 2010) than the red-tailed monkey groups (~0.35 km^2; this study, see *Methods*). Chimpanzees live in fission-fusion communities, such that individuals frequently join with and separate from other individuals as they move throughout the home range in pursuit of food, social opportunities, and other factors (Potts et al., 2015, 2016). In general, chimpanzee diets and physical condition (Emery Thompson et al., 2009), activity budgets (Doran, 1997), travel patterns (N'guessan et al., 2009), and social behavior (Mitani et al., 2002) closely track the availability of valuable ripe fruits. Chimpanzee movements target productive areas (Wrangham, 1977), leading to uneven use of their extensive home range (Potts et al., 2015). As a result, the presence and number of chimpanzees within a red-tailed monkey group

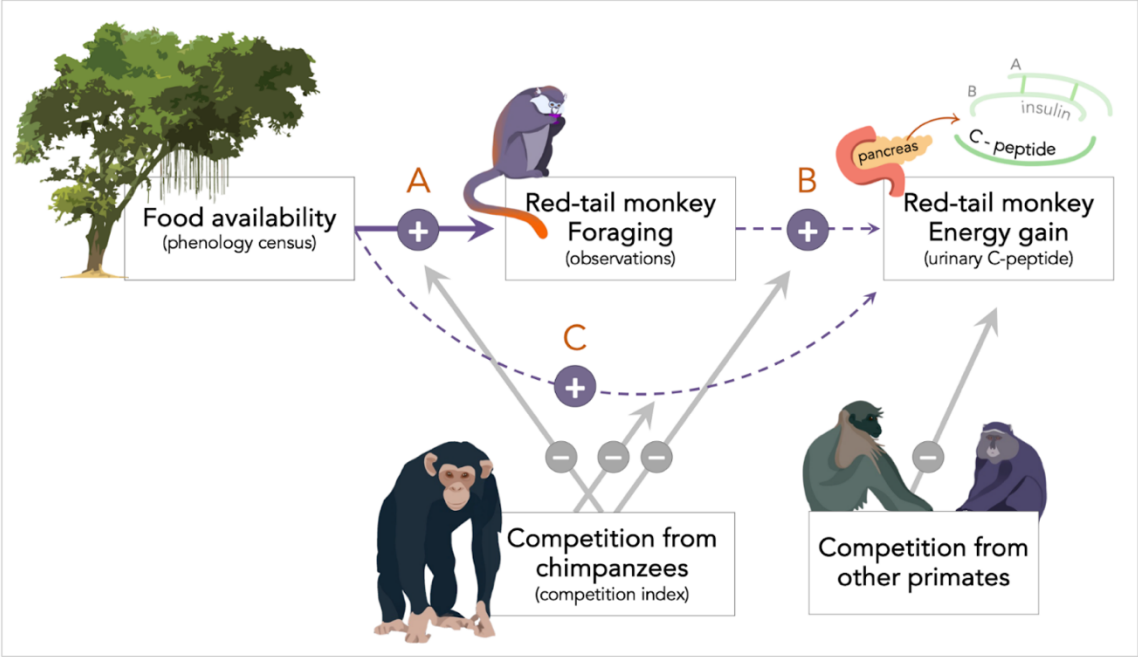

Figure 2.1. Movement of Energy from Environment to Individual. Directed acyclic graph representing the relationships among environmental pressures and behavioral and physiological outcomes for red-tailed monkeys: food availability on foraging behavior (**A**), foraging on energy gain (**B**), and food availability on energy gain (**C**). Feeding competition from chimpanzees modifies these relationships, and competition from other primates affects energy gain. Purple arrows represent positive predicted relationships (e.g., when fruit is abundant, foraging on fruit should also increase). Gray arrows represent negative relationships (e.g., competition from chimpanzees should reduce or reverse energy gain as a result of food availability). Thick solid arrows represent relationships that were statistically significant in this study, and thin dashed arrows represent relationships that were not statistically significant (see Tables S2.4, S2.6, S2.7).

home range fluctuates over time. Chimpanzees also opportunistically hunt and consume red-tails (McLester et al., 2019; Watts & Mitani, 2002), causing the monkeys to avoid chimpanzees by freezing (often for hours) or fleeing to the far side of their home range, far from preferred food sources (McLester, 2020). This twofold cost of an intraguild predator (Amarasekare, 2008; Holt & Polis, 1997) constrains the monkeys' ability to pursue and access available resources. We hypothesized that, for red-tailed monkeys, access to food resources should depend on the presence of chimpanzees in their home range; as a result,

their energetic and reproductive outcomes should correspond with the combined effects of competition from chimpanzees and food availability, especially ripe fruit (Figs. 1, 2b).

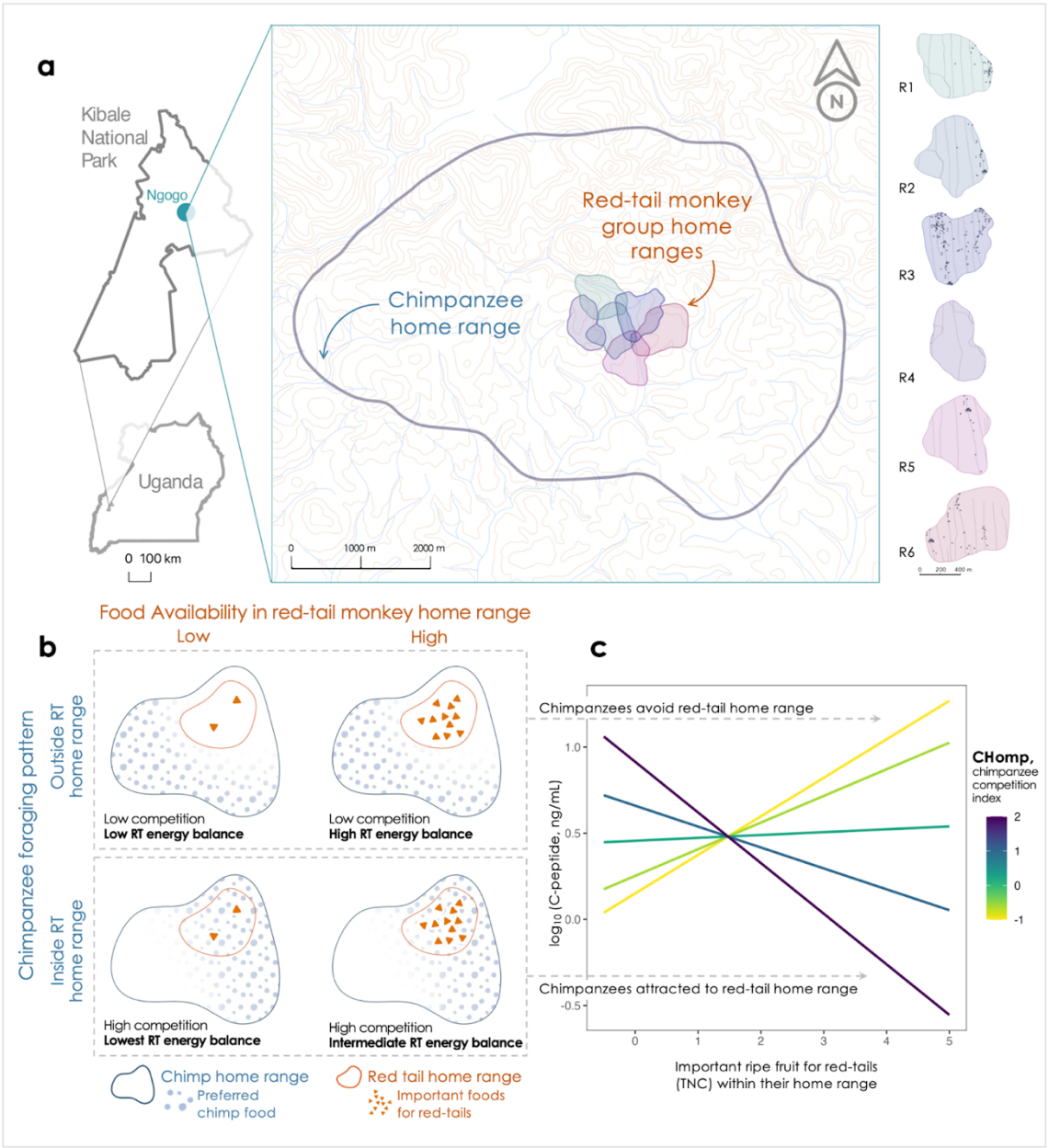

Figure 2.2. Red-tailed monkey energy balance is strongly modified by feeding competition from chimpanzees. a) Home ranges of six groups of red-tailed monkeys within the chimpanzee community home range at the Ngogo site in Kibale National Park, Uganda. Gray vertical lines within the red-tail home ranges (far right side of the panel) are trails that were walked during monthly red-tail phenology censuses, and the dots within each range are individual trees surveyed during monthly chimpanzee phenology censuses. We calculated the chimpanzee competition (CHomp) index using a subset of trees from the chimpanzee phenology census that fell within each red-tail home range. **b)** Theoretical

model with the predicted effects of different combinations of food availability and feeding competition on red-tailed monkey energy balance. **c)** Observed pattern of red-tailed monkey energy balance (measured as urinary C-peptide levels) in relation to the availability of important ripe fruits (total nonstructural carbohydrates; TNC in g) for red-tails in their home ranges, and modified by varying feeding competition from chimpanzees. Colored lines indicate fitted values from a multilevel model, with each color indicating a different intensity of chimpanzee competition.

To measure the effects of interspecific feeding competition on red-tailed monkeys, we evaluated a biomarker of individual energy balance (E_B), which is the surplus of energy consumed from food sources minus energy expenditures. We measured E_B via radioimmunoassays of urinary C-peptide, which is a by-product of insulin production and a biomarker that offers a precise, non-invasive measure of E_B (Emery Thompson & Knott, 2008; Sherry & Ellison, 2007). As individuals feed on carbohydrate-rich fruits and their circulating glucose increases, diurnal C-peptide levels spike. We collected urine samples (N = 1,228) non-invasively and recorded the feeding behavior of adults (78 F, 7 M) and sub-adults (17 F, 12 M) from six groups of red-tailed monkeys at the Ngogo Research Station in Kibale National Park, Uganda (latitude 0.502' N, longitude 30.424' E) from 2012 through 2015 (Fig. S2.1b). C-peptide levels did not differ among age (adult, subadult) and sex (F, M) classes (ANOVA, $F_{3, 1224}$= 1.02; P = 0.38; Fig. S2.3; congruent with Sherry & Ellison, 2007), so all age-sex classes were combined for subsequent analyses.

The chimpanzee community range is ~100 times larger than a typical red-tail home range (Mitani et al., 2010; Fig. 2.2a), and fruiting patterns are ephemeral and variable across valleys within the range. Chimpanzees tend to focus their foraging efforts in areas of their home range that consistently provide high yields of ripe fruits, which plays a key role in shaping their movement and habitat use (Potts et al., 2015, 2016; Wrangham, 1977). Thus, we assumed that chimpanzees would be attracted to individual red-tail study group home ranges

when the latter contain valuable chimpanzee foods, and that chimpanzees would avoid the monkey ranges when such foods are absent (Fig. 2.2b). Due to their predictable preference for these productive regions, we use the abundance of preferred chimpanzee foods as a proxy for their foraging and *ranging behaviors* (Janmaat et al., 2014; Normand et al., 2009; Wrangham, 1977). When valuable chimpanzee foods are scarce in the red-tail home range, red-tail E_B should track the availability of important red-tail foods (P_0). However, as the abundance of valuable chimpanzee foods increases within the red-tail home range, we expect the relationship between food availability and E_B for red-tails to weaken and even reverse due to the competitive and predatory effects of chimpanzees (P_1). This prediction also suggests that the presence of other primate competitors – i.e., grey-cheeked mangabeys (*Lophocebus albigena*) and blue monkeys (*Cercopithecus mitis*), which are intermediate in size between red-tails and chimpanzees, and do not consume red-tails – will also correlate negatively with red-tail E_B. However, the effect of the presence of larger monkeys is likely to be less dramatic than the effect of chimpanzees because red-tails actively pursue associations with these other monkey species (Bryer et al., 2013), implying that the *energetic cost* is outweighed by benefits such as anti-predation advantages (Chapman & Chapman, 2000) from *polyspecific associations*.

We measured the monthly availability of foods consumed by red-tails within their home ranges, as well as a proxy for the intensity of feeding competition from chimpanzees. We then compared a set of multi-level linear regression models (Table S2.1; *lme4* package in R; Bates et al., 2015; R Core Team, 2020) using an Information Theory approach (Burnham & Anderson, 2002) to determine whether red-tailed monkey C-peptide levels correlated with food availability and chimpanzee competition. We measured red-tail food availability in terms of nutrients (total non-structural carbohydrates, TNC in grams), quantity (estimated

number of fruits), or total mass (biomass in kg) of fruit, and did so for different plant parts (ripe and unripe fruits, as well as flowers) and different sets of plant species (important red-tailed foods, which are plants that made up >10% of the monthly diet of at least one social group, and non-important plant foods). We estimated feeding competition from chimpanzees (hereafter '*CHomp*') as the abundance of valuable chimpanzee foods within an individual red-tail home range. We used Akaike Information Criteria (AIC) to compare models with different combinations of predictors and determine which food types interact with competition from chimpanzees to best predict red-tail energy gain.

Of all the models we tested, only one (model 1; 2 S2.1) fell within the confidence set of best-fit models (Table S2.3), which we then expanded to include the effect of competition from other fruit-eating primates (grey-cheeked mangabeys and blue monkeys ; Table S2.4). On its own, the availability of important ripe fruits does not affect red-tail E_B ($\beta = 0.05$, CI = -0.06, 0.17, $p > 0.05$). Instead, red-tail E_B is shaped by the interaction of CHomp and food availability: when fruit availability increases, the effect of CHomp is higher, and red-tail E_B declines (P_1); conversely, when CHomp is weak or absent, red-tail E_B increases with ripe fruit availability [P_0, $\beta = -0.17$, CI = -0.29, -0.05, $p = 0.005$; Fig. 2.2c, Table S2.4]. CHomp not only affects the overall relationship between food availability and red-tail E_B (interaction; gray arrow pointing at relationship C in Fig. 2.1) but also the subsumed relationships between food and foraging (interaction; gray arrow pointing at A in Fig. 2.1; IRR = 0.22, CI = 0.13, 0.38, $p < 0.001$; Fig. S2.5, Table S2.7-*TNC / Ripe Fruit*) and foraging and E_B (interaction; gray arrow pointing at B in Fig. 2.1; $\beta = 0.30$, CI = 0.16, 0.45, $p < 0.001$; Fig. S2.4, Table S2.6). Neither flowers, which are high in rapidly digestible sugars (Bryer, 2020), nor unimportant ripe fruits, which offer a viable substitute when red-tails cannot access preferred foods (Lambert & Rothman, 2015), have a distinct effect on E_B.

This pattern of results challenges conventional assumptions that greater food availability translates directly to better nutritional or energetic status for smaller species mired in competition (Raubenheimer et al., 2009; White, 2008) and underscores the complexity of ecological interactions in determining primate health and behavior. The presence of chimpanzees fundamentally alters whether and how red-tails benefit from food availability. Additionally, the time spent in polyspecific associations with other, larger monkey species had mixed outcomes: red-tail E_B decreased when they spent more time with mangabeys (β = -0.20, CI = -0.32, -0.09, p = 0.001) but not with blue monkeys (β = 0.13, CI = -0.13, 0.38, p > 0.05). These findings suggest that while forming associations with other species might offer some ecological advantages, such as decreased time allocation to vigilance or increased information about food sources (Bryer et al., 2013), associations with mangabeys might impose additional competitive pressures that ultimately detract from the nutritional benefits otherwise available to red-tailed monkeys. The differential impacts of chimpanzees, mangabeys, and blue monkeys underscores the complexity of primate communities and the nuanced ways in which these associations influence energy balance. When mangabeys are present within a red-tail home range, the red-tails pursue close-range associations with them up to 83.5% of the time (the proportion of group scans per group and per observation period in which the group was observed ≤ 50 m from managabeys; min = 1.4%, mean = 30.1%), while only up to 31.6% for blue monkeys (min = 0.4%, mean = 8.9%). These ranges indicate that the benefits and costs of polyspecific associations are not uniform but instead depend on the species involved, their dietary needs, population density, and possibly their expression of competitive behaviors.

These findings highlight a critical ecological insight: the impact of food availability on primate nutrition cannot be fully understood without considering the competitive landscape.

The movement of primates in their habitat is shaped by a complex interplay between foraging decisions (aka the *"landscape of energy"*; Gallagher et al., 2017) and predation risk (aka the *"landscape of fear"*; Laundré et al., 2010). To avoid predators, red-tails may forgo resource-rich areas or spend more energy traveling in pursuit of lesser foods. This involves a continuous decision-making to weigh the costs of energy expenditure against the risk of encountering predators (Gallagher et al., 2017). Red-tails face a dilemma when they must compete for limited resources with their potential predator. The expectation is that they should be excluded from resource-rich environments due to this combined pressure (Amarasekare, 2008; Holt & Polis, 1997). While fruit availability does not exert a main effect on red-tail energy balance, its positive impact emerges when chimpanzees avoid their home range. Consumers must adapt their foraging behavior to maintain a more positive energy balance, but their ability to do so is influenced by the active choices of competitors, especially under the risk of intraguild predation. The crux of red-tails' coexistence alongside intraguild predators that limit their energy gain hinges on their competitive strategies (Holt & Polis, 1997)– i.e., their ability to navigate the landscape of fear and still find and rapidly exploit food before it is accessed by competitors, which has been documented in red-tails at Ngogo (Waser & Case, 1981).

The ecological and social environment of red-tailed monkeys is shaped by a web of interactions that includes not only the relatively obvious and costly competition for resources with more dominant species like chimpanzees, but also the complex dynamics of polyspecific associations with heterospecifics, which likely includes costs and benefits in different currencies. The contrasting impacts of mangabeys and blue monkeys highlight the importance of species-specific approaches in determining the outcomes of such interactions. Identifying these dynamics provides deeper insight into how red-tailed monkeys navigate

their ecological niche and manage energy resources in the face of interspecific competition. Future research is needed to identify the effects of non-primate competitors (e.g., fruit bats, hornbills, and other frugivores) on the energy landscape for red-tails and other small-bodied primates.

Competition in primate communities occurs at multiple levels–i.e., within groups, between groups, and between species–significantly shaping their social and ecological dynamics. Our findings underscore the importance of considering competition not only within and between social groups (intraspecific competition), but also, critically, between species when evaluating primate behavior. Because of their highly social nature, research on primate feeding competition has predominantly focused on intraspecific dynamics. However, our study reveals that interspecific competition can have profound and often greater impacts on individual energy gain, a main driver of fitness. Just as observed in other taxa (e.g., invertebrates: Neumann & Pinter-Wollman, 2022; fish: Maruyama et al., 2010; amphibians: Borzée et al., 2016; birds: Thornton et al., 2015; rodents: Meng et al., 2023; Mitchell et al., 1990; group-living carnivores: Watts & Holekamp, 2008), the presence of dominant competitors like chimpanzees significantly alters the relationship between food availability and energy intake in red-tailed monkeys, demonstrating that interspecific interactions are not merely background noise but pivotal factors shaping ecological outcomes. These results complement and extend the existing body of research, suggesting that integrating interspecific competition into models of primate behavior can enhance our understanding of the complexities of their ecological and social environments. Most primate species coexist among heterospecifics (Schreier et al., 2009) and are threatened with extinction (Estrada et al., 2017). Examining underexplored ecological factors that profoundly affect population dynamics, such as competition and intraguild predation, can make conservation strategies

more robust, enhancing the survival and resilience of species (Wang et al., 2024). This approach can also better equip them to maintain species richness and ecosystem services despite the quickening pace of habitat degradation and climate change (Guillaumet & Russell, 2022). By incorporating these interactions, future studies can provide a more comprehensive view of the factors driving primate population and community dynamics.

2.2 METHODS

2.2.1 Study Site and Species

Kibale National Park is a mid-elevation, moist evergreen rainforest in western Uganda, spanning 766 km^2 (Chapman et al., 2000), and consists of a mosaic of various successional stages - including large portions of old-growth rainforest, secondary forest, early- and mid-stage colonizing forests, freshwater swamp, and grasslands (Lwanga et al., 2000; Potts, 2008; Struhsaker, 1997). We conducted this study at the Ngogo site which experiences an average annual rainfall of 1427mm, though there is high variability in rainfall among months, seasons, and years (Potts et al., 2020). Red-tailed monkeys at Ngogo live in stable social groups consisting of multiple adult females, their offspring of varying ages, and one adult male. The total number of adult and sub-adult members per study group varied from 13 to 28 (mean $\pm$ SD = 19.2 $\pm$ 5.7). Red-tail groups appear to be food-limited and frequently fight over access to fruit trees (Brown, 2013; Brown et al., 2022). They seek out ripe fruit but are often observed eating unripe fruit from the same plant species (Bryer, 2020; Struhsaker, 2017).

2.2.2 Behavioral Observations

M.B. and a team of field assistants conducted the fieldwork for this study from December 2011 through June 2015 as part of a study of intergroup conflicts with conspecifics (Brown, 2014; Jaeggi et al., 2018). They recorded behavioral observations and collected urine samples from 108 adult and subadult individuals in six groups of habituated red-tailed monkeys. During the study, six females transitioned from the subadult to the adult age class; subadults are defined as having a body size nearly as large as adults and are not yet reproductively active with adults. Each animal was identifiable using the unique shape of the white nose spot; distinctive scars, stiff fingers, and tail kinks; and for females, the length, size, and color of nipples. Observers followed two groups simultaneously for 3-6 months, then switched to another pair of groups for several months. Each group was followed at least twice during the 3.5 years of observations (Fig. S2.1). During a multi-month observation period, observers followed the groups from dawn until dusk every day for one or two weeks, then rested for a week before resuming observations. On follow days, they recorded the group's location as the center-of-mass position every 30 minutes, along with foraging and polyspecific association data (Fig. S2.2). Observers had 5 minutes at the start of each 30-minute interval to record all foraging activity, including monkey identification, part eaten (unripe or ripe fruit, young or mature leaf, flower, insect, or other), tree species, location, and diameter at breast height. Polyspecific associations were recorded if heterospecifics were within 50 meters of the red-tail group, which is a common definition of polyspecific proximity in the literature (Klein & Klein, 1973; Rijksen, 1977; Struhsaker, 1981).

2.2.3 Phenology

Two separate projects measured phenological food availability at Ngogo simultaneously (Fig. S2.2). The Ngogo Monkey Project recorded data using a red-tail phenology census, representing all fruit available for a red-tail group within its home range, during every 1-2 week long observation period. An observer walked along existing north-to-south trails within the focal group's range and recorded the quantity and species of unripe and ripe fruits of all tree, liana, and shrub species within 1 m of each side of the trail (Fig. 2.1a). Crop size estimates of the number of individual fruit per species and per trail segment were binned into logarithmic categories (0, 1-9, 10-99, 100-999, *sensu* Leighton, 1993) to balance accuracy against human counting error. The Ngogo Chimpanzee Project monitored fruit production on 20 stems of each of 38 tree species that are important for chimpanzees (Watts et al., 2012). Chimpanzee communities exhibit highly dynamic fission-fusion behavior, making exhaustive data on their ranging during specific periods difficult to obtain (Watts, 1998). Field assistants follow individual or pairs of chimpanzees for short periods before switching to different individuals. However, data on the entire community is necessary; the presence of even a single chimpanzee near fruiting trees or their noise poses a threat to red-tails, and initiates behavioral responses (Teelen, 2007; Watts & Mitani, 2002). Chimpanzees travel to and forage in high-yield areas within their home range, reliably prioritizing regions with abundant preferred ripe fruits, which strongly influences their movement patterns and habitat use (Potts et al., 2015, 2016; Wrangham, 1977). Given their predictable reliance on these productive areas, we use the chimpanzee phenology census dataset as a proxy for chimpanzee foraging and ranging patterns (Janmaat et al., 2014; Normand et al., 2009; Wrangham, 1977). The percentage of each tree crown bearing ripe fruit was recorded as one of five abundance categories (no fruit, 1-25%, 26-50%, 51-75%, or 76-100%, on a scale of 0-

4, respectively; Chapman et al., 1994). The red-tail- and chimpanzee phenology censuses shared 30 species in common out of the combined 76 species (Table S2.8).

2.2.4 Urine Collection and Analysis

Observers sampled urine opportunistically and noninvasively from adult (963 samples from females, 110 from males) and subadult (60 F, 95 M) individuals during group follows (Fig. S2.2), with a target of 2-3 samples per monkey, per month. They collected 1,366 samples total, of which 1,228 were used in this study after excluding samples for which corresponding phenological or behavioral data were absent. Observers collected samples by placing clean plastic sheeting under the individual as it urinated, or by pipetting urine from low-lying vegetation immediately after excretion (Emery Thompson & Knott, 2008). An observer carried the urine samples to camp at 1700 hrs and stored them in a -12°C solar-powered freezer. M.B. transported samples to the Hominoid Reproductive Ecology Laboratory at the University of New Mexico, where they were stored in a -30°C freezer until analysis. M.B. measured specific gravity on thawed samples using a digital refractometer (Atago PAL-10S, Omaeda, Japan) to correct C-peptide values from samples of varying concentrations (Anestis et al., 2009; Miller et al., 2004); all C-peptide values are hereafter reported in units of nanograms of the C-peptide protein per milliliter (ng/mL). M.B. assayed urinary C-peptide for each sample in duplicate using a commercial human C-peptide radioimmunoassay kit (Millipore Corporation, Billerica, MA), which was cross-validated for use with non-human primate samples (Emery Thompson et al., 2009; Emery Thompson & Knott, 2008; Sherry & Ellison, 2007). Due to highly variable C-peptide concentrations, many samples were run multiple times at different dilutions (from 1:1 up to 1:50) until the adjusted concentration of C-peptide fell within the standard binding curve. Assay accuracy, as

determined by the recovery of a sample added in duplicate to all points of the standard curve, was 101.8 ± 1.5% (mean ± std dev, N = 6). Parallelism was verified by comparing binding from serial dilution of a sample (y = -47.4x + 183.8) to the standard curve (y = -45.9x + 179.8, t = 0.432, df = 8, P = 0.677). Intra-assay coefficient of variance (CV) was 2.4% and inter-assay CV of low and high controls was 4.4% and 8.3% (N = 51 batches).

2.2.5 Data Wrangling

Geospatial analysis and mapping were performed in the Quantum Geographic Information System platform (v. 3.36.0; QGIS Development Team, 2024). All data analysis was done in R (v. 2023.12.1.402; R Core Team, 2021; RStudio Team, 2020). Data exploration and visualization used packages from the *tidyverse* (v. 2.0.0, Wickham et al., 2019). Models were evaluated using the *lme4* package (v. 1.1-35.1, Bates et al., 2015) and model output tables (Tables 2.1, 2.3) compiled using *sjPlot* (v. 2.8.15, Lüdecke, 2021). Model evaluation using Akaike Information Criteria for small samples (AICc; Table 2.2) was performed using the *AICcmodavg* package (v. 2.3.3, Mazerolle & Mazerolle, 2017).

We pooled red-tail foraging data by group and observation period (Fig. S2.1a, S2.2) to calculate diet summaries with the goal of identifying important food items (including ripe and unripe fruit, uncategorized fruit–i.e., fruit of unknown ripeness state, flowers, young leaves, and insects), defined as those constituting ≥10% of the monthly diet of at least one group in any observation period. Among the 68 plant species recorded in the red-tail phenology census, 30 were identified as 'important foods' by this criterion (Tables S2.1). Fruit and flowers are the primary drivers of variation in E_B (Knott, 1998; Ross et al., 2022), so we excluded other food types when foraging was used as a predictor in these analyses (Table S2.2). For the regression analyses, we also calculated the proportion of daily foraging

on particular food items out of all foraging observations per-group (N = 750 group-days), i.e., the number of times that item was observed eaten during group scans relative to all feeding observations that day. Polyspecific association data were calculated per red-tail group, per day, as the proportion of 30-minute group scans in which the red-tail group was ≤50 m from each species. We calculated the home range of each group as the 95% kernel density estimate of all center-of-mass points of that group in R (Fig. 2.1a; *adehabitatHR* package; Calenge, 2006; R Core Team, 2020). Subsequent spatial analysis and mapping were performed in QGIS (QGIS Development Team, 2024).

We were uncertain whether red-tail E_B would correspond with the number of fruiting bodies, their summed mass, or the sum of readily digestible carbohydrates, so we converted the red-tail phenology data into all three measures (Fig. S2.2). The quantity of fruit is the simplest measure to calculate, but has relatively low biological relevance because some fruiting bodies are miniscule and others are massive (range: 0.11 - 1,958.00 g). The summed mass of fruit is more appropriate, but not all fruit parts have the same nutritional value. The sum of readily digestible carbohydrates should have the highest biological relevance, assuming red-tails are targeting fruit with high energy content, but is far more difficult to calculate and has more sources of error (see description below), limiting its accuracy as a measure of fruit availability.

To calculate biomass, we recorded fruit and seed mass from ripe and unripe fruits (at least 3 fruits per ripeness to determine mean mass values per stage, per plant species). Missing mass values were supplemented using mean values from surveys of plant-based monkey foods in Kibale National Park in 1992-1993 and in 2015-2016 (Conklin-Brittain et al., 1998; Bryer, 2020). For each plant species, we multiplied the fruit weight (excluding inedible parts) by the summed crop sizes per monkey home range and observation period.

To determine the quantity of available red-tail fruit, we used the median of each crop size category (e.g., if 1-9 ripe fruit were recorded for a particular species, we used an estimate of 5 fruits) and summed all records within the home range in a given observation period (Fig. S2.2). We then calculated the quantity of easily digestible sugars in the red-tail home ranges. We gathered nutritional data (total nonstructural carbohydrates, TNC; % dry weight/100g) for ripe and unripe fruit of different plant species from Bryer (2020), R. W. Wrangham (unpublished data from Conklin-Brittain et al., 1998), Potts (2008), and McLennan & Ganzhorn (2017). Where direct values of energy were missing (N = 5 species), we inferred values using records of other nutrients (crude protein (CP), available protein (AP), non-digestible fiber (NDF), lipids, and TNC) with the Atwater formula for food energy conversion (Conklin & Wrangham, 1994; Conklin-Brittain et al., 2006; Rothman et al., 2012). We included mean NDF digestibility coefficients from red-tailed monkeys studied at another research site in the same forest (Bryer, 2020). We supplemented missing AP values using mean crude protein values: i.e., we calculated the mean AP:CP ratio per plant family and ripeness stage (ripe or unripe), then multiplied by the CP value to provide the best estimate of available protein. Missing AP values for plants of families different than those in existing data were estimated using the mean AP:CP value from all plants of the same ripeness stage. The TNC value per plant species was multiplied by its measured biomass and summed per home range to produce an estimate of the absolute amount of energy (TNC) within the home range per observation period.

We used data collected during a plant phenology census conducted by the Ngogo Chimpanzee Project to approximate the intensity of chimpanzee competition (CHomp) within each red-tail home range per month (Fig. S2.2). Due to the different methods employed by each research group, this census yielded different values from the red-tail

census for the abundance of ripe fruit per species per red-tail home range per month. Thus, the data from the two censuses are not collinear. The CHomp variable is based on the availability of ripe fruits from plant species preferred by chimpanzees, and is calculated as a fruit availability index (FAI). To track monthly fruit availability, the Ngogo chimpanzee researchers use phenology data from 20 stems of each of 38 species fed upon by chimpanzees at Ngogo (Watts et al., 2012). The percentage of the tree crown bearing fruit is logged in five abundance categories (no fruit, 1-25%, 26-50%, 51-75%, or 76-100%, or a scale of 0-4, respectively), multiplied by its diameter at breast height (DBH) and then by the density of its species in the habitat to calculate a monthly ripe fruit score (Mitani et al., 2002). To calculate the chimpanzee FAI as the competition index, CHomp, for each red-tail group, we used data only for trees from this census that fell within the home range of each group or within a 100 m buffer zone around the home range because primates perceive predators as a threat at a distance of up to 100m (Ducheminsky et al., 2014; Stankowich & Blumstein, 2005).

The resulting per-redtail-group subset of the chimpanzee phenology data represents only a fraction of the trees across the chimpanzees' larger home range. We omitted tree species density when calculating the FAI because habitat-wide estimates of densities would not necessarily represent the distribution within the relatively small and highly heterogeneous home ranges of the red-tails. For example, *Milletia dura*, a fruiting tree species that is highly important for chimpanzees, occurs at a density of 7.7 stems per hectare throughout the habitat (Chapman et al., 1999), while it has 14 stems in the homerange of red-tail group R1 and only 1 stem in the home range of group R6. DBH generally correlates with fruit yield (Miller & Dietz, 2004), so for each tree in a given month, we multiplied its ripe fruit score only by its DBH and summed across species to yield the FAI per red-tail home range per

month (Chapman et al., 1992; Fig. S2.2). Lastly, the monthly chimpanzee phenology census was not synchronized with the red-tail behavioral observation periods. As a result, a particular chimpanzee census might occur during or between monkey observation periods. We determined the number of days of overlap between a monthly chimpanzee FAI value and a red-tail observation period and used it to weight the FAI to produce a per-observation period *CHomp* index.

2.2.6 Outliers

In a preliminary analysis of our dataset of 1,228 urine samples, we encountered several statistical outliers. Six C-peptide observations corresponded with a single phenology value that significantly diverged from the norm (fruit availability measured in TNC, z-scored: min = -0.23, mean = 0.00, max = 5.82), suggesting potential data entry errors due to their substantial deviation from the rest of the data. Further examination of the red-tail phenology dataset of 18,672 observations helped trace these outliers to a single month with an abnormal value of *Monodora myristica* fruit abundance. A Grubb's test ($p << 0.001$) flagged this record for its extreme biomass value of 962.5 kg (from an estimated 550 individual fruits) in one 50-meter-long stretch of the monkey phenology census trail. This value lies far beyond the remainder of the right-skewed dataset, which corresponds to the episodic nature of fruit production in forest trees. Such an extreme outlier was not supported by any biological or ecological observations. Unlike the approximately 100 observations identified through interquartile range (IQR; Tukey, 1977) analysis as exceeding the 1.5*IQR threshold (Pollet & van der Meij, 2017)— all of which were biologically plausible and retained to account for genuine environmental variability — this single phenology data point was excluded to maintain analytical integrity. Its removal was substantiated by sensitivity analyses,

which revealed a skewed perception of fruit availability effects by an overstated 15%, highlighting the critical impact of such an outlier on our findings. The decision to exclude this single outlier was based on statistical evidence and an understanding of this plant species' biological capacity, ensuring that the retained data accurately represent the natural variability inherent in our study's environmental context.

2.2.7 Statistical Analyses

Potential analytical approaches to evaluating the relationships in this study would be structural equation models or path analyses (SEM; Mitchell, 1992). SEMs generally require large sample sizes to produce reliable results. However, the different datasets used in this study (chimpanzee phenology, red-tail phenology, C-peptide, foraging, and polyspecific associations) vary in spatiotemporal scales. Reducing them to a common scale results in a highly limited dataset (N = 63 group-periods), losing a substantial amount of variation. Similarly, the non-linear structure of relationships in this study (Fig. 2.1) further compounded the small sample size, making a path analysis less suitable (Wootton, 1994; Mitchell, 1992). Instead, we opted to run several sets of mixed-effect regression analyses (Galecki et al., 2013) to effectively capture the relationships between variables, which allow us to address both individual- and group-level variation.

To determine whether red-tailed monkey C-peptide levels correlated with fruit availability (arrow C in Fig. 2.1), and whether feeding competition from chimpanzees affected this relationship, we compared a set of linear mixed-effect models (*lme4* package in R; Bates et al., 2015; R Core Team, 2020) using an Information Theory approach (Burnham & Anderson, 2002). We used the C-peptide value per urine sample, adjusted by specific gravity, as the response variable; as this variable spanned five orders of magnitude and was

left-truncated (mean = 10.31 ± 22.31 ng/mL), we $\log_{10}$-transformed the values. Outliers (other than the single phenology datapoint mentioned above) were not excluded from analyses because the distribution is primarily normal and right-skewed, with some values above the upper boundary of the interquartile range, indicating that the existence of higher values is not statistically abnormal (Aguinis et al., 2013). Additionally, we assumed that the inclusion of other parameters in the multi-level models would explain this variation (Langford & Lewis, 1998).

We used month and red-tail group identity as crossed random effects (Galecki & Burzykowski, 2012). We initially also included 'Individual ID,' the unique name for each red-tailed monkey, as a random effect but removed this term after it prevented models from converging (Bolker et al., 2009). We evaluated six measures of fruit availability, each representing a unique combination of ripeness (ripe versus unripe), and method of measurement (TNC, quantity, and biomass; Tables S2.1, S2.2). Each model included fruit availability terms for both important and unimportant fruit species within the monthly diet. This approach was necessitated by several factors. First, visual inspection of the raw data indicated that ripe and unripe fruits might exhibit opposing relationships with C-peptide. Second, as noted above, we were unsure which measure of monkey fruit availability (TNC, quantity, and biomass) would prove to be both relevant and accurate. Third, while 'important' species constitute the bulk of red-tail energy intake and foraging effort, 'unimportant' fruit might yet be relevant because less-frequently eaten fruit species may also contribute to C-peptide and foraging patterns. We evaluated subsets of these predictors to avoid collinearity among certain terms. Each model contains two measures of fruit availability (important and unimportant fruits, calculated from the red-tail phenology census), a measure of chimpanzee competition (calculated from the chimpanzee phenology

census) and an interaction between two of the terms. We ran an Eigensystem analysis and found no multicollinearity between these terms (R Core Team, 2020; Shrestha, 2020). We excluded a term for the unimportant unripe fruit from model *TNC – unripe* (Table S2.2; Table S2.3, model 2) because we did not have sufficient nutrient data for unripe fruits that are rarely or never consumed by red-tails. This term was kept for the biomass and quantity models because phenology data exists for these fruit items. We also considered a null model containing random effects but no fixed effects. We standardized all fixed-effect predictors. We then evaluated the models based on their AIC weights (ω_i; Burnham and Anderson, 2002; Table S2.3). The confidence set of best-fit models includes those with ω_i scores within 10% of the highest-ranked model (Burnham & Anderson, 2002).

2.3 Ethical Statement

Permissions to conduct this study were granted by the Uganda Wildlife Authority, the Uganda National Council for Science and Technology, and the Uganda Office of the President. Data collection protocols were approved by the Institutional Animal Care and Use Committee of the University of New Mexico (11-100661-MCC). We conducted all research activities in compliance with Ugandan national laws and ASAB/ABS guidelines for the use of animals in research.

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III. Remote Sensed Vegetation Indices Predict Frugivorous Primate Behavior and Energetics in Tropical Rainforests

3.1 Introduction: Seeing the Forest for the Trees

3.1.1 Importance and Current Methods of Estimating Food Availability

A major challenge in behavioral ecology is uncovering the mechanisms that govern the distribution and internal dynamics of animal populations over space and time. Food availability, one of the most important factors in an animal's life, is a pivotal factor in wildlife ecology and directly influences the survival, growth, and reproduction of animals (McNab, 1980; Prevedello et al., 2013), including fruit-eating primates (Emery Thompson, 2017). The nutritional content of food resources dictates the amount of energy that is available for essential biological processes (Lambert & Rothman, 2015), but it varies greatly over time and between plant food species, stems of the same species, and even within the crown of a single tree (Houle et al., 2014). The fickle nature of nutrient fluctuations complicates our ability to decipher the intricate dynamics between wild animals and their environments (Cleland et al., 2007; Houston et al., 2007). This challenge is intensified for primates, whose diets are highly diverse and flexible (Lambert & Rothman, 2015). It also underscores the need for strong phenological predictions–i.e., the timing of different stages of plant growth, such as leaf flushing or fruiting in plants– that accurately represent the environment in which primates live. This necessity is especially urgent in the context of primate conservation, given how vast environmental changes have reduced the availability of resources and have left about two-thirds of the world's primate species at risk of extinction (Estrada et al., 2017). However, common measures of food abundance do not always reflect what some primates,

especially subordinate ones, can access (see Chapter 2 of this dissertation). Thus, novel tools are needed to draw a better picture of the habitat from the perspective of a small-bodied primate. Here, we test how well remote-sensed data on habitat productivity predicts fruit availability and foraging behavior in fruit-eating primates in tropical rainforests.

A substantial amount of effort has gone into fine-tuning how we measure energy and nutrient intake for primates, especially at the individual-level. Nutrient and energy intake vary not only with the seasonal appearance of fruit in their habitat, but also with the constantly shifting *nutritional landscape* in which they live (Houle et al., 2014; Rothman et al., 2012). Precise estimates entail measuring the exact quantity of calories, and micro- and macronutrients consumed and absorbed, an infeasible task in wild, and largely arboreal animals. The best approximation that exists necessitates measuring habitat-wide fruit availability (e.g., the biomass of fruit in a given area) and sampling the bite-rates of individual animals over a lengthy period (Rothman et al., 2012), which is a profoundly labor-intensive method, especially when sampling multiple groups and species. While estimating fruit availability and distribution is crucial to understanding primate behavior (Isbell, 1991; Kappeler & van Schaik, 2002; Terborgh & Janson, 1986; Wrangham, 1980), the time-honored methods of on-the-ground phenological assessments are labor-intensive and provide only limited insights (Chivers, 1998), especially in the challenging terrain of tropical rainforests (Marshall & Wich, 2013). Phenological surveys do not account for interspecific dynamics that limit a species' access to preferred food resources (see Chapter 2). Interspecific dominance hierarchies, differences in foraging patterns, and navigating the risk of predation (i.e., the *"landscape of fear"*; Gallagher et al., 2017) create discrepancies between resource availability (a species' fundamental niche) and accessibility (its realized niche; Hutchinson, 1957; Pulliam, 2000), rendering different energetic and nutritional landscapes

for species occupying the same habitat. Additionally, the temporal and spatial scales of phenological monitoring are typically too coarse to gain a true estimate of the amount of resources that are available. The goal of phenological censuses is to identify general trends or changes in food abundance along a given transect line or in a given area (Marshal & Wich, 2013), which is typically much smaller than a group's home range, and which presumably underrepresents the true botanical diversity and heterogeneity of the habitat. Periodic censuses might miss the occurrence of ephemeral, yet highly valuable resources in between sampling periods. Moreover, the shifting nature of the nutritional composition of individual plant species or fruiting bodies means that a food item that was desirable in the past might not be as desirable or nutritionally valuable today (Rothman et al., 2015). Increased surveying effort does not necessarily overcome these issues, as they are further compounded by the aforementioned limitations in accurately capturing the amount of calories and nutrients that primates consume and absorb (Chivers, 1998; Houle et al., 2014).

Fine-tuning the accuracy of counting fruiting bodies or the precision of measuring nutrients in the habitat represents an extensive undertaking that is beyond the scope of this dissertation and does not necessarily solve the issue of the time- and labor-intensive nature of phenological surveying (Gray & Ewers, 2021). Instead, we seek novel, less demanding methods that might bypass some of the limitations in evaluating habitat productivity discussed above. Remotely sensed data and vegetation indices (VIs) have emerged as promising tools for bridging this gap (Turner et al., 2003). Applying a broader perspective, they offer a less laborious means of mapping large-scale phenological events and understanding the relationships between environmental conditions and primate behavior and health (Chambers et al., 2007; Handcock et al., 2009).

3.1.2 Vegetation Indices

Among the many remotely monitored environmental variables (such as climate, soil characteristics, and land surface temperatures), few are as valuable to terrestrial ecologists as variables related to plant productivity and phenology. Remote-sensed VIs have become more common in recent decades in studies of wildlife (Gray & Ewers, 2021; Kerr & Ostrovsky, 2003; Oeser et al., 2020; Turner et al., 2003), enhancing our understanding of the effect of environmental conditions on biodiversity (Jetz et al., 2019; Ruggiero & Kitzberger, 2004), movement patterns (Ruegg et al., 2006; Rumiano et al., 2020), and even life history (Rasmussen et al., 2006; Wittemyer et al., 2007). The Normalized Difference Vegetation Index (NDVI) is one of the most commonly used VIs (Rouse Jr et al., 1974; Tucker, 1979). NDVI captures reflectance contrasts in the visible red and near-infrared (NIR) spectral domains, where plants absorb red light for photosynthesis but reflect NIR light, an attribute that is invisible to humans, yet crucial for remote sensing. In areas with high plant biomass, high NDVI values generally correspond to mature, healthy leaves, and low values to new or young leaves (Rapaport et al., 2014). This is because mature leaves have fully developed mesophyll structures, a spongy tissue inside the leaf that scatters NIR light effectively, while absorbing red light due to higher chlorophyll content, the pigment responsible for photosynthesis. In contrast, young leaves, although rich in chlorophyll, often lack fully developed mesophyll structures that maximize NIR scattering (Wang et al., 2012). Therefore, mature leaves contribute more to the high contrast between NIR and red reflectance, resulting in higher NDVI values. As tree canopies change seasonally from an early growth phase to late-season maturity, their reflectance properties also change, contributing to the NDVI of the habitat. NDVI is typically measured at a temporally frequent, yet spatially coarse resolution, generally larger than the size of a single tree's crown (see *Methods*, below),

so it represents a composite environmental estimate. As a result, the overall NDVI value in a particular area is dependent on the botanical composition and quality of the habitat (Pettorelli et al., 2005), which also corresponds to the potential abundance of food sources for plant-eating animals, like primates (Lambert & Rothman, 2015). Consequently, NDVI is a well-established correlate of vegetation biomass, photosynthetic activity, and vegetation productivity (Li et al., 2021; Myneni et al., 1995; Shammi & Meng, 2021; Shi et al., 2017), and is often used to contextualize trophic interactions and animal behavior (Pettorelli et al., 2005). NDVI is also offers a comprehensive five-decade-long dataset, publicly available from various monitoring agencies, including NASA's Earth Observation System - Terra Satellite (NASA, 2022), making it particularly valuable for long-term ecological studies. The instruments on the satellites capture data continuously and provide global coverage every 1-2 days, offering high-frequncy sampling of data, which is then rendered into multi-day or multi-week averages to remove variability in measurements caused by cloud coverage.

The utility of NDVI in studies of animal behavior and ecology are thoroughly documented (Pettorelli et al., 2011), but it has limited efficacy in tropical rainforests because it saturates in areas of high biomass. While NDVI provides a measure of canopy greenness and is effective for broad environmental monitoring, the Enhanced Vegetation Index (EVI; Huete et al., 2002) is optimized for areas with high biomass and provides highly accurate and more robust estimates of *primary productivity* (Rahman et al., 2005). It expands on the NDVI by incorporating a blue spectral band to improve sensitivity by reducing soil and atmospheric background influences. EVI also adjusts for canopy structure effects, and unlike NDVI, it does not saturate in areas with high biomass (Huete et al., 2002), making it more effective in tropical rainforests (Galvão et al., 2011). Because of its inherent reliance on the size and color of leaves, EVI is predominantly used in studies of herbivores that rely highly

on leaves or other plant foliage (i.e., folivores). For example, EVI is shown to correlate with folivore dietary quality and preferences (Villamuelas et al., 2016), foraging behavior (Benedetti et al., 2023), home range use (Axel et al., 2024), and even reproduction (Texeira et al., 2012). However, EVI has the potential to be used as a predictor of such characteristics in frugivorous primates as well, because in controlled environments (e.g., agricultural plots), it provides a strong estimate of plant phenological cycles and correlates positively with the biomass of fruit crops (De Petris et al., 2019; Rahman et al., 2022; Son et al., 2014). Additionally, larger trees, which take up more physical space and therefore contribute more significantly to local EVI values than smaller ones, typically produce more fruit biomass (Minor & Kobe, 2019), thereby linking EVI values to food abundance for frugivores. In natural habitats, EVI has been used to determine cues for migratory behavior in fruit-eating birds (Papeş et al., 2012), predict patterns of fruit-bat species diversity along gradients of forest connectivity (dos Santos et al., 2016), and more recently to determine habitat requirements in frugivorous primates (Steffens et al., 2023), with direct applications for targeted species management and conservation. The growing support for its use in studies of frugivores highlight the potential of EVI as a strong tool in studies of primates, even for the most frugivorous of populations.

While VIs have long been employed in ecological studies of non-primates (Pettorelli et al., 2011), they have not yet been used to estimate food availability for frugivorous primates in tropical forests. Where remote-sensed VIs have been used successfully to predict primate foraging or behavior, they are typically limited to either folivorous primates (e.g., sifakas; Axel et al., 2024) or those living in relatively open and dry environments (e.g., vervets, baboons: Findlay & Hill, 2020; García et al., 2022; crowned lemurs: Steffens et al., 2023). Linking EVI with the behavior of frugivorous, rainforest-dwelling primates represents a

novel approach and an attempt to refine our understanding of how measurements of fruit availability can be optimized to advance the study of these complex animals.

3.1.3 Measuring Energy Balance in Primates

The key to determining whether VIs capture food availability as seen through the eyes of the consumers depends on measuring energy consumption more proximately, by looking at the consumer's energy gain (Fig. 3.1). Measuring energy gain can provide a comprehensive picture of the combined energy and nutrients that primates obtain from their habitat. However, accurately measuring primate energy intake is an arduous undertaking, due to the high variability in primate diets and the difficulty in capturing precise nutrient and calorie consumption (Houle et al., 2014; Rothman et al., 2012).

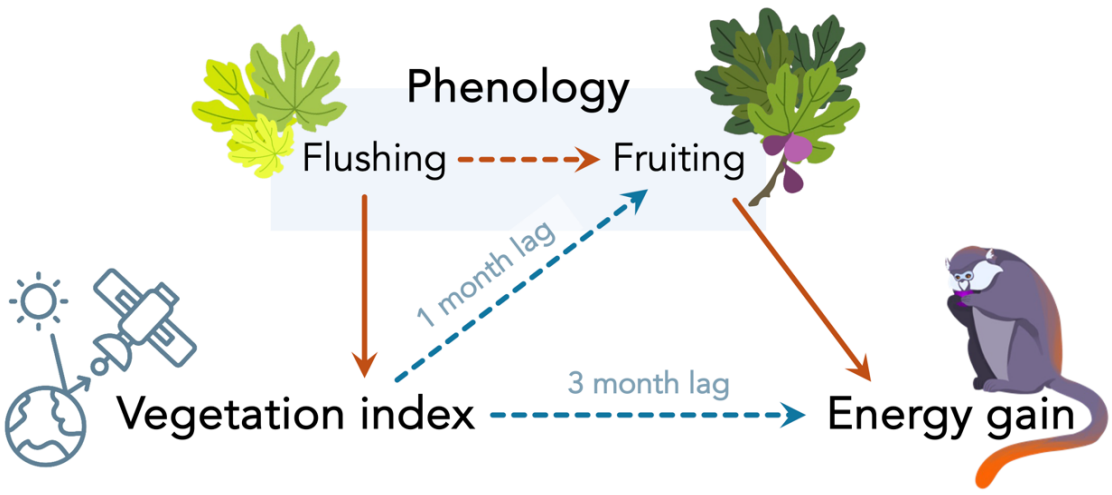


Figure 3.1. Diagram of relationships between variables. Conceptual model of the relationship between phenological timing of vegetative (flushing) and reproductive (fruiting) phases of plant growth, remote-sensed enhanced vegetation indices (EVIs), and primate net energy gain via consumption of ripe fruit. The solid arrows represent immediate relationships, and the dashed arrows represent time-lagged relationships. Orange arrows represent relationships we do not test in this chapter, while the blue relationships are evaluated in this study for their utility in primate research. The lag durations noted along the dashed blue lines are the lag approximations corresponding to the strongest models in our analyses (Tables 3.1 and 3.3).

Traditional methods are invasive and stressful (Baylis et al., 2015; Speakman, 1997), while non-invasive alternatives often lack precision (Pontzer, 2015). However, recent advancements in endocrinology show promise in overcoming these limitations. C-peptide of insulin is a by-product of insulin production and is thus sensitive to circulating glucose levels from energy-dense foods, like fruit. It provides an accurate measure of net energy gain in primates (Emery Thompson & Knott, 2008). Unlike insulin, it is immediately excreted in urine, can be collected non-invasively (see *Methods*), and is easily assayed using commercially available kits. Urinary C-peptide (UCP) reflects an individual's physical condition (Emery Thompson, 2017), and higher values are indicative of periods of energy surplus. A positive energy balance (E_B), indicates that the individual is consuming more energy than they are expending, which is typically a response to an increase in the quantity or quality of food items consumed. By evaluating UCP against EVI we connect remote-sensed habitat monitoring and individual behavior (Fig. 3.1), both of which are understudied in rainforest-dwelling, frugivorous primates.

3.1.4 Novel Approach

Primate populations are limited by food availability (Hanya & Chapman, 2013), a correlate of primary productivity which can be reliably monitored in tropical rainforests using VIs (Galvão et al., 2011). EVI's enhanced accuracy over NDVI makes it particularly valuable for studying tropical rainforests, where most primates live (Napier & Napier, 1985). These remote-sensed data can capture critical phenological changes in rainforests, such as the transition from leaf flushing (plant investment in growth) to fruiting (plant investment in reproduction; Rapaport et al., 2014) in flowering and fruiting trees (i.e., angiosperms). The most notable change in EVI occurs in the months following peak litterfall (the loss of old

leaves from the canopy), between the appearance of young leaves and their subsequent maturation (Xiao et al., 2005). When leaves are mature, fruiting trees can prioritize fruit production (Obeso, 2002). The temporal scale of this change can be used as an indication of the time lag between leaf flushing, when EVI values are lowest, and the time at which foraging and an increase in energy balance occur, when EVI is peaking and when urine is sampled (Fig. 3.1). The lag between leaf flushing and fruiting is on average about 2.5 months in African rainforests (van Schaik & Pfannes, 2009), but can last about 1.5-4 months, depending on the plant species. Our study aims to leverage these observations to calibrate and improve the use of EVI as a predictor of frugivorous primate foraging behavior. We expect that high UCP values will correlate with low EVI values 2.5 months prior (van Schaik & Pfannes, 2009). We perform a lag analysis and evaluate consecutive EVI values over time to find the lag at which EVI can serve as a precursor of increase in energy balance in frugivorous primates in a tropical rainforest.

The lag-analysis of remote-sensed estimates of habitat productivity is a novel and potentially powerful approach for several reasons. First, it capitalizes on the heavily documented phenological timing of plant growth and reproduction in tropical rainforests, which is applicable for most primate species (Napier & Napier, 1985). It also considers foraging at the most proximate level– i.e., increases in energy balance– through the use of metabolic hormones as a direct measure of fruit consumption (Emery Thompson & Knott, 2008). Lastly, it uses remotely sensed data to overcome the limitations of current fruit availability measurement methods in many studies of primate feeding ecology (Chivers, 1998; Marshall & Wich, 2013).

In this study, we evaluate the relationships between EVI, human-monitored phenological records, and UCP values from red-tailed monkeys (*Cercopithecus ascanius*)

collected over approximately four years from six social groups of red-tails at the Ngogo Research Station in Kibale National Park, Uganda. We hypothesize that high values of EVI, which indicate leaf maturation and a shift to fruiting phase, will correspond with increases in fruit abundance and the corresponding increase in energy balance. Alternatively, the emergence of young leaves (EVI minimum) could be a stronger predictor of energy balance due to EVI's sensitivity to capturing changes in phenological phases. Mature leaves, which are consistently abundant in tropical rainforests (Clark et al., 2015), likely establish the baseline EVI in a habitat. It is the periodic drop in EVI that accompanies new growth that leads to a significant change that is more easily identified, and which is highly correlated with fruiting approximately 2.5 months later. These two possibilities are not mutually exclusive. By examining EVI as a predictor of fruit availability and its subsequent impact on primate energy balance, we aim to evaluate this VI as a more accurate alternative to traditional phenological methods for measuring fruit availability, which could significantly improve our understanding of primate biogeography.

3.2 METHODS

3.2.1 Study Site

We evaluated VIs within the home ranges of six groups of red-tailed monkeys at the Ngogo Research Station (0.502' N, 30.424' E). Ngogo is situated deep within Kibale National Park, a mid-elevation moist evergreen rainforest in western Uganda, which spans 766 km^2 (Chapman et al., 2000; Struhsaker, 1997). Ngogo consists of a mosaic of various successional stages including large portions of old-growth rainforest, secondary forest, early- and mid-stage colonizing forests, freshwater swamp, and grasslands (Lwanga et al., 2000;

Potts, 2008; Struhsaker, 1997). This region of Uganda experiences two wet seasons spanning roughly March-May and September-November, separated by two dry seasons, with an average annual rainfall of 1427mm, though there is high variability in rainfall among months, seasons, and years (Potts et al., 2020). Plant species diversity is relatively high compared to similar sites in the Congo Basin, but lower than in tropical lowland evergreen forests (Potts et al., 2020; Potts & Lwanga, 2014). Plants exhibit fairly continuous community-level fruiting but with small, irregular annual fruiting peaks that occur heterogeneously across space and time (Chapman et al., 2005; Chapman & Chapman, 1999; Potts et al., 2020). The result is high seasonality in fruiting patterns throughout the forest, with significant spatial discrepancies even in neighboring valleys.

3.2.2 Study Species and Behavioral Observations

Red-tailed monkeys are small-bodied (males: 3.7, females: 2.8 Kg; Cords et al., 2013) arboreal primates endemic to sub-Saharan tropical forests in East and Central Africa. Their primary habitat is moist lowland, submontane, or montane forests, and they thrive in both regenerating and primary forests, especially along forest edges (Cords & Sarmiento, 2013). Vast differences in foraging patterns have been observed between populations, neighboring social groups, and even within a group over time (Bryer, 2020; Chapman et al., 2002; Struhsaker, 2017), and though they predominantly seek out ripe fruit, they are often observed eating unripe fruit, leaves, flowers, and other plant parts. Like many other fruit-eating primates, red-tails live among one or more food competitors (Struhsaker, 1978; Waser & Case, 1981) in habitats characterized by rapidly changing nutritional landscapes (Houle et al., 2006, 2014). To minimize the costs of feeding competition, they evolved highly diverse and seasonally fluctuating diets (Bryer et al., 2015; Chapman et al., 2002), with increased

reliance on insects during lean periods (Struhsaker, 2017). Red-tails offer a unique opportunity to study the connection between remote-sensed data and energy balance because their broad and flexible diets are representative of those of many other primate species (Chivers, 1980), including endangered and under-studied species.

Red-tails at Ngogo live in stable social groups of up to 30 individuals, consisting of multiple adult females, their offspring of varying ages, and one adult male. The samples and data used here were originally collected as part of a study on red-tailed monkey energetics at Ngogo, and detailed information can be found in previous publications (Brown et al., 2022; Steinitz et al., *in prep*, and Chapter 2 of this dissertation). We studied six habituated groups (18.17±5.18 adults and subadults per group) that are located centrally within the research station study area, with adjacent and slightly overlapping home ranges (mean 0.37±0.04 km^2; Fig. S3.1).

M.B. and a team of field assistants conducted the fieldwork from December 2011 through June 2015 as part of a study of intergroup conflicts with conspecifics (Brown, 2014; Jaeggi et al., 2018). Observers followed two groups simultaneously for 3-6 months, then switched to another pair of groups for several months. Each group was followed for multiple consecutive months at least twice during the 3.5 years of observations (Fig. S2.1 in Chapter 2). Observers followed the groups from dawn until dusk every day for one or two weeks (hereafter, "observation periods"), then rested for a week before resuming observations.

3.2.3 Biomarker Data

Detailed sample collection and analysis methods follow those of Emery Thompson & Knott, 2008 and are described in detail in Steinitz et al., *in prep* and in Chapter 2 of this

dissertation. To summarize, we sampled urine opportunistically and noninvasively from adult (1,062 urine samples from females and 127 from males) and subadult (73 F, 104 M) individuals during group follows, with a target of 2-3 samples per monkey, per month (N = 1,366 samples total from 109 individuals). We followed each group on average for eleven hours per day and collected urine from identified individuals. Samples were kept on ice in an insulated container until we returned to camp and then stored at -12°C until they were exported back to the Hominoid Reproductive Ecology Laboratory at the University of New Mexico. We measured specific gravity using a digital refractometer (Atago PAL-10S, Omaeda, Japan) to standardize C-peptide (UCP) values across varying urine concentrations (Anestis et al., 2009; Miller et al., 2004). UCP values hereafter are reported in units of nanograms of the C-peptide protein per specific gravity (ng/mL). We assayed UCP in duplicate for each sample using a commercial human C-peptide radioimmunoassay kit (Millipore Corporation, Billerica, MA), validated for non-human primate samples (Emery Thompson et al., 2009; Emery Thompson & Knott, 2008; Sherry & Ellison, 2007). Chemical validations are detailed in Steinitz et al., *in prep*.

3.2.4 Phenological Data

We used the same methods approach detailed in Chapter 2 (Steinitz et al., *in prep*) to track variation in fruit availability within the home ranges of red-tail groups; we conducted a phenology census to record the quantity and species identity of ripe fruits along existing trails within each group's home range once every observation period. To estimate the amount of energy available for red-tails, we converted the phenology data into three measures, calculated per home range, per observation period: a) quantity, as the estimated number of ripe fruiting bodies; b) biomass (in kg), as each plant species' average ripe fruit

mass, multiplied by its summed ripe fruit crop size per home range, and then summed across plant species; and c) total nonstructural carbohydrates (TNC in g), which is a measure of readily digestible sugars in fruit. Each measure has different levels of biological relevance, calculation complexity, and error structure, with quantity being simplest but least representative of the energetic and nutritional landscape; biomass being more accurate but not representative of nutritional values; and TNC being most relevant but hardest to calculate accurately.

In the phenology census, an observer recorded the quantity and species of unripe and ripe fruits within 1 meter of the sides of the north-to-south trails in the group home range (Chapter 2, Fig. 2.1a). Fruit crop estimates were binned using logarithmic categories to balance accuracy with counting error (Leighton, 1993). We estimated ripe fruit quantity by using the median of each crop size category and summing all records within the home range during each observation period. We calculated biomass by recording fruit and seed mass from at least three ripe fruits per plant species to determine mean mass values per stage. Missing fruit mass values were supplemented using surveys from Kibale National Park (1992-1993, 2015-2016; Bryer, 2020; Conklin-Brittain et al., 1998), and for each plant species, we multiplied the fruit weight (excluding inedible parts) by the summed crop sizes per monkey home range and observation period. We obtained TNC values from Bryer (2020), R. W. Wrangham (unpublished data), Potts (2008), and McLennan & Ganzhorn (2017), and calculated missing values from other available nutritional values using the Atwater Formula for Food Energy Conversion (Conklin & Wrangham, 1994; Rothman et al., 2012). Species-specific TNC values per gram were multiplied by the biomass calculated per plant species per home range to produce an estimate of the absolute amount of rapidly-digestible sugars that are available for consumption within each home range in every observation period.

3.2.5 Remote-sensed Data

Vegetation index data were obtained from NASA's Earth Observing System Data and Information System (EOSDIS) database (NASA, 2022). NASA Terra satellite's Moderate Resolution Imaging Spectroradiometer (MODIS) generates two primary vegetation indices (MOD13Q1) – a NDVI and an EVI – every 16 days at a 250-meter spatial resolution (Didan, 2015). EVI is calculated from spectral bands as follows:

$$EVI = G \times \frac{(NIR - Red)}{(NIR + C_1 \times Red - C_2 \times Blue + L)}$$

where G is a scaling (gain) factor that is used to improve the sensitivity of the index in areas with dense vegetation; NIR, Red, and Blue are atmospherically corrected (Rayleigh and ozone absorption) surface reflectances for the respective spectral bands; L is the canopy background adjustment that addresses nonlinear, differential NIR and red radiant transfer through a canopy; and C_1, C_2 are the coefficients of the aerosol resistance term, which uses the blue band to correct for aerosol influences in the red band. The coefficients used in the EVI algorithm are, L=1, C_1=6, C_2=7.5, and G=2.5 (Huete et al., 1997). EVI ranges from -1 to +1 (Huete et al., 2002), where negative numbers indicate an absence of vegetation. Pre-consumer data processing involves selecting the best pixel values based on low cloud presence, minimal view angle, and the highest index values, ensuring a consistent and accurate representation of vegetation states.

3.2.6 Data Analysis

Geospatial analysis and mapping were performed in the Quantum Geographic Information System platform (v. 3.36.0; QGIS Development Team, 2024). Maps were composed using a satellite world imagery base layer (Esri, 2009) and a topographical contour

base layer generated from the Uganda 30m SRTM Digital Elevation Model (Esri, 2018). Data analysis was done in R (v. 2023.12.1.402; R Core Team, 2021; RStudio Team, 2020). Data exploration and visualization used packages from the *tidyverse* (v. 2.0.0, Wickham et al., 2019). Models were evaluated using the *lme4* package (v. 1.1-35.1, Bates et al., 2015) and model output tables (Tables 3.1, 3.3) compiled using *sjPlot* (v. 2.8.15, Lüdecke, 2021). Model evaluation using Akaike Information Criteria for small samples (AICc) (Table 3.2) was performed using the *AICcmodavg* package (v. 2.3.3, Mazerolle & Mazerolle, 2017).

3.2.6.1 Spatial Data

We converted remote-sensed data to home-range specific weighted EVI means per 16-day cycle (matching the timing and duration of the cycles of the original EVI dataset; Didan, 2015) using a multi-step approach. First, red-tail group home range shapefiles were generated using 95% kernel density estimates (*adehabitatHR* package; Calenge, 2006) in R (R Core Team, 2021; RStudio Team, 2020). These estimates were based on each group's center of mass recorded at 30-minute intervals from dawn to dusk during every day of observation (approximately 11 hours per day) by our team (detailed information in Steinitz et al., *in prep*). The home range shapefiles were then imported into QGIS (Fig. 3.2), where they were overlaid with a 250x250m grid raster of EVI values derived from MODIS satellite imagery (NASA, 2022; Didan, 2015). The raster cells were vectorized and clipped to match the extent of the home range. Raw EVI values must be scaled using VI-specific scaling factors to generate an index between -1 and +1, so we multiplied the raw EVI value of each cell by 1×10^{-4} (MODIS Vegetation Indices scaling factor; Didan, 2015; Huete et al., 2002). We then created a weighted mean EVI value per home range: each cell's value was multiplied by its area (km^2), summed for each home range per 16-day cycle, and the sum was divided by the

total area of the home range. This calculation resulted in a single mean EVI value for each group's home

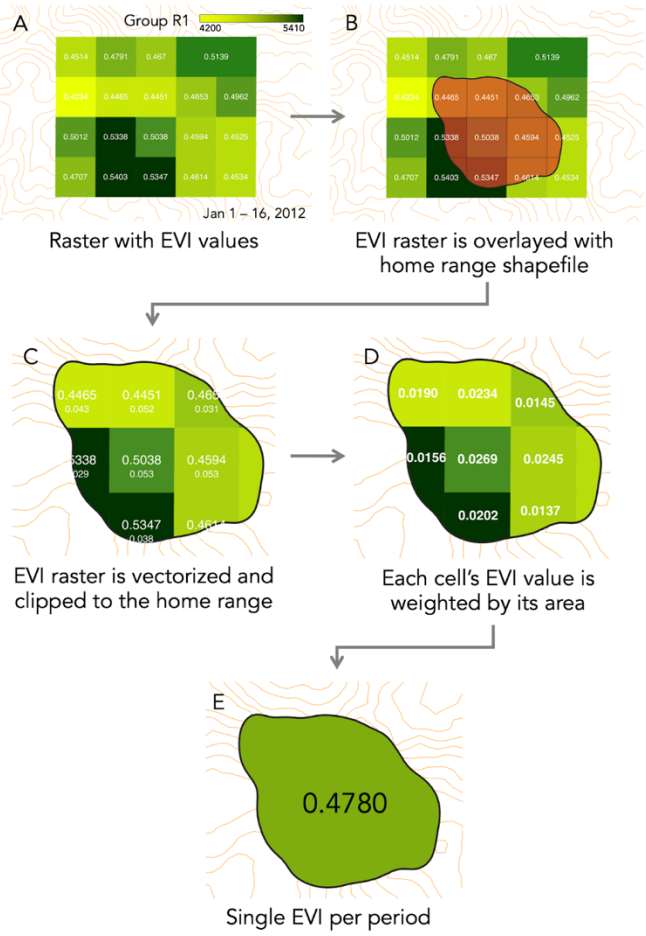


Figure 3.2. Calculation of EVI per Home Range. Schematic representation of the method for calculating weighted mean Enhanced Vegetation Index (EVI) values within red-tailed monkey home ranges. A raster containing a 250x250m grid of EVI values derived from MODIS satellite imagery (**A**; e.g., recorded between January 1-16, 2012) is overlayed with the home range shapefile specific to the red-tailed monkey group R1 (**B**). The EVI raster is subsequently vectorized and clipped to match the extent of the home range (**C**). The large-text value is the EVI score for the grid cell and the smaller value below is the cell area within the home range in km^2. Each cell's EVI value is then weighted by the proportion of its area within the total area of the home range (**D**), and all values are summed and divided by the sum of the weights (the total area). The final output is a single weighted mean EVI for the specified semi-monthly period, representing the average vegetation condition within a red-tailed monkey group home range during that period (**E**). EVI rasters were sourced from the MODIS/Terra satellite's 16-day composite product at a spatial resolution of 250 meters (Didan, 2015). The light to dark green gradient of the raster grid represents the range of EVI values from low to high.

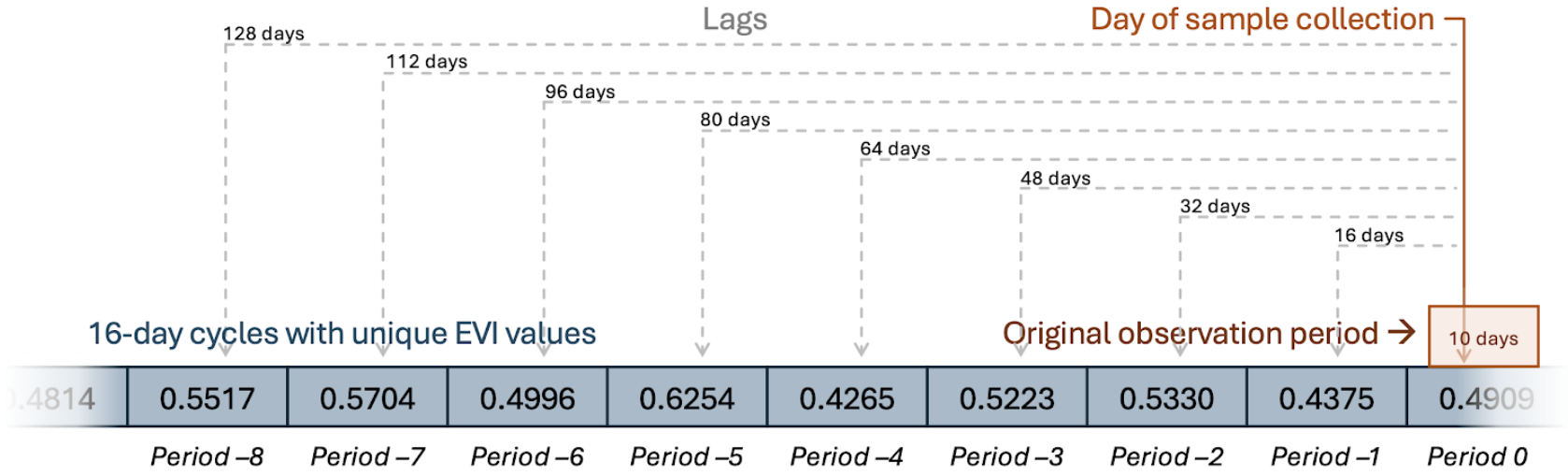
range for each 16-day cycle throughout the entire study period (December 2011 – July 2015; 82 cycles each for 6 red-tailed groups, totaling 492 group-cycles).

3.2.6.2 Time Scales and Lags

We performed a lag analysis to evaluate both the fundamental utility of EVI as a predictor of fruit availability and primate energy balance, and the time frame at which this interaction occurs. Phenology data are collected once every observation period, so analyses with phenological data as an outcome are referenced to the median day of the observation period (*Period 0*), and subsequent lags were calculated backward from this date (Fig. 3.3). UCP data are evaluated as group mean per day, because doing so smooths out error while allowing for nuanced evaluation of short-term fluctuations. Group daily means reflect the reality of sample collection, where samples are often sparse, necessitating pooling multiple values to minimize error and represent inter-individual variation. Conversely, the group-day approach (compared to weekly or monthly means) also allows for a nuanced evaluation of short-term energetic fluctuations caused by highly ephemeral food resources (ripe fruit, which is quickly depleted), or from foods abnormally high in easily digestible sugars (e.g., blooms of flowers; Ross et al., 2022).

We evaluated EVI at 16-day intervals (lags) to match the nature of the publicly-available EVI data commonly used in ecological studies and because semi-monthly cycles effectively capture dynamic changes in fruit production and availability. Fruit development often spans several weeks, making semi-monthly intervals suitable for capturing these patterns (Cardoso

Figure 3.3. Structure of the lag analysis. Schematic of sequential time lags from the observation period up to 128 days (roughly 4.25 months) before the date of sample collection. The structured lag analysis helps assess the delayed effects of habitat quality on primate energy balance. *Period 0* (orange rectangle) indicates the duration of the original 10-day observation period during which the group was followed, urine samples were collected, and phenology was recorded. Each Enhanced Vegetation Index (EVI) value represents aggregated values from 16-day cycles from NASA MODIS dataset (see *Methods – Remote-sensed Data*). The EVI value for *Period 0* is referenced from the day of sample collection. The EVI values for previous periods (*Periods –1* through *–8*) correspond to increasingly larger time lags between the day of sample collection and individual EVI cycles (i.e., lags; dashed gray lines). Each cycle has a unique EVI value (gray rectangles) calculated per group home range from the MODIS data (Fig. 3.2), aggregated at 16-day intervals. The time lag, represented as $Lag_{Period\text{-}i} = 16 \times i$ indicates the number of days between the sample collection period and the semi-monthly period of evaluation.



et al., 2019). This approach provides a balance between temporal resolution and practical feasibility, ensuring that important biological events are not overlooked. The lag analysis included time lags from sequential semi-monthly (16-day) EVI cycles extending back approximately four months from each observation period (*Period –1* through *Period –8*; Fig. 3.3). The time lag, represented as, $Lag_{Period\ -i} = 16 \times i$, indicates the number of days between the sample collection period and the semi-monthly period of evaluation.

3.2.6.3 Model Structure

We omitted observations that lacked EVI data for every lag. For example, observation periods from January of 2012 did not have corresponding lag data from EVI lags in 2011 (i.e., any lags > 16 days, *Period –1*), so these rows were omitted from analyses. Additionally, fewer group-days were available than the expected 660 (66 group-periods x 10 days each) because samples were not collected on every day of observation. In total, there were 469 group-days for UCP models (Table 3.1). Phenology analyses using TNC values were further reduced due to missing nutritional data for some plant species, leading to no data during certain group-periods and their exclusion. Consequently, the datasets included 66 group-periods for quantity and biomass phenology models and 62 group-periods for TNC phenology models (Table 3.3).

To test the utility of EVI as a predictor of red-tail energy balance and the temporal scale at which EVI can provide insight on primate behavior, we ran four sets of linear mixed-effect regression models (*lme4* package v. 1.1-35.1, Bates et al., 2015). The first set of models evaluated mean group UCP per day in response to EVI as a fixed effect. Each model in the

set included a single EVI term, and the set encompasses the sequentially increasing lagged EVI terms (*Period 0* through *Period –8*; Fig. 3.3; Table 3.1). We then ran three parallel sets of models testing the temporal relationship between EVI (in similar sets of lagged EVI term) and the phenological timing of reproductive (fruiting) phases of plant growth (Fig. 3.1; Table 3.3). Each set used one estimate of fruit availability (FAI, biomass, and TNC) as the outcome variable. All models included 'group identity' as a random effect and all but the TNC models included 'observation period' as well. We initially also included 'observation period' as a random effect in the TNC models, but removed this term after it prevented models from converging (Bolker et al., 2009). Confidence intervals (95% CI) and p-values were computed using Wald tests (Phillips, 1986).

In addition to the primary analysis, I explored a Bayesian hierarchical approach to evaluate the relationship between EVI and UCP, focusing on the 75-day marker with lags of approximately 64, 80, 96, and 112 days. This analysis compared mean, max, and weighted sum EVI values to assess their predictive power. Further details on the choice of predictors, the Bayesian models, and results are available in the supplemental materials.

3.3 RESULTS

Model comparison using the small sample Akaike Information Criteria (AICc; Burnham & Anderson, 2002) indicated that the EVI value in *Period –6*, 96 days prior to urine sampling, best correlated with C-peptide values (Fig. 3.4), showing a strong negative relationship with UCP (β = -1.34, CI = -2.42, -0.27, p = 0.015; Table 3.1; Fig. 3.5), with 51.8% of the variance explained by the model (conditional R^2 = 0.518; Table 3.1). Akaike weights indicated that this model was 18% better at predicting UCP than the next best lag model (64 days prior, *Period –4*; Table 3.2). Interestingly, a different period correlated more strongly with phenology; EVI

from 32 days prior to the observation period had a strong negative relationship with the amount of ripe fruit production in the home range, measured in

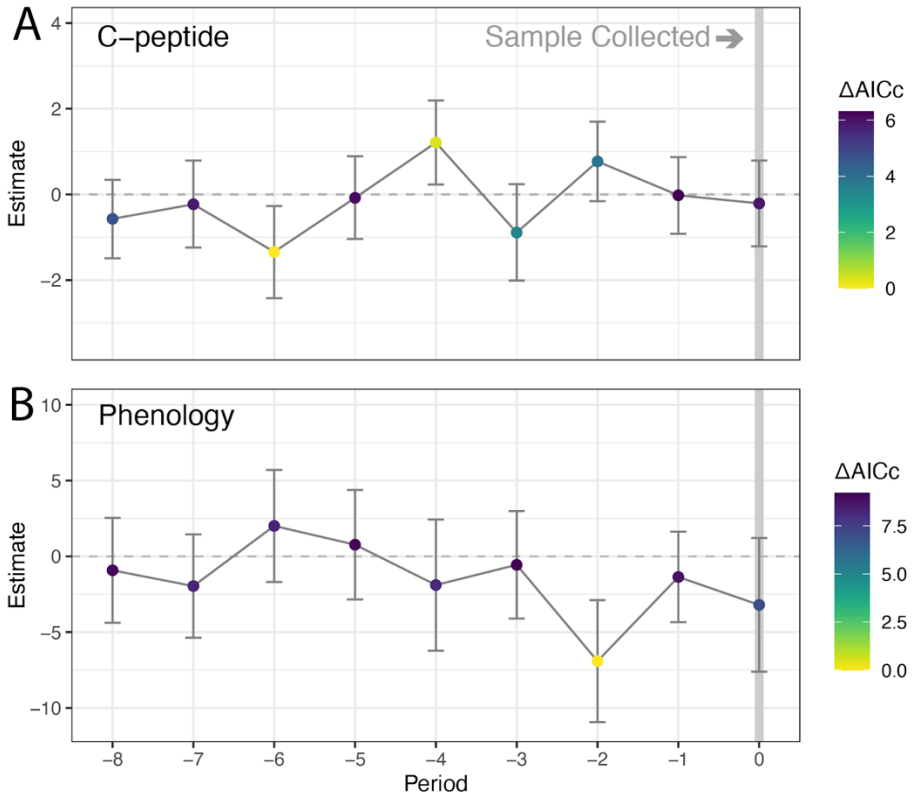


Figure 3.4. Model estimates and ΔAICc Comparison. Model estimates and 95% confidence intervals for two sets of linear mixed-effect regression models testing the relationship between an Enhanced Vegetation Index (EVI) and two outcome variables (*sensu* Morgan et al., 2023): A) red-tailed monkey group mean energy balance (urinary c-peptide, ng/mL) per day, and B) ripe fruit availability (Phenology; Biomass, kg) per observation period. The graphs depict the oscillating nature of the relationships between EVI and the response variables, and the direction of these relationships depends on the time lag. Each point with whiskers in the panels represents an estimate ± 95% confidence intervals from an individual model (Table 3.1). *Periods 0* through *–8* represent the sequential lags (Fig. 3.3) corresponding to the 16-day cycles at which EVI is reported (MODIS/Terra satellite's 16-day composite product; Didan 2015). Point color represents ΔAICc values–the difference of the model's AICc from that of the strongest model in the set (*Period –6* for C-peptide, and *Period –2* for Phenology). Thick gray lines represent the period in which samples and phenological data were collected. See Tables 3.1 and 3.4 for model details.

Table 3.1. VIs as predictors of energy balance. Linear mixed-effect regression models of the relationship between enhanced vegetation indices (EVI) and red-tailed monkey energy balance. Energy balance is the group mean of log10-transformed urinary c-peptide values (UCP ng/mL) per day from six red-tail groups. The models evaluate EVI, calculated for each observation period (Period 0), and extend backward sequentially in 16-day cycles (*Period –1* through *Period –8*; see Figure 3.3) from the beginning of the observation period. σ^2 = Mean random effects variance; τ_{00} = Random intercept variance: observation period & group; R2M = Marginal R2; R2C = Conditional R2; AICc = Akaike information criterion. The shaded column denotes the strongest model (Table 3.2).

	Period 0	**Period -1**	**Period -2**	**Period -3**	**Period -4**	**Period -5**	**Period -6**	**Period -7**	**Period -8**
Intercept									
Estimate	0.41	0.32	-0.08	0.75	-0.29	0.35	0.96	0.42	0.59
CI	-0.14, 0.97	-0.18, 0.82	-0.60, 0.45	0.14, 1.35	-0.82, 0.25	-0.18, 0.88	0.39, 1.54	-0.13, 0.96	0.09, 1.09
p	0.141	0.208	0.770	**0.016**	0.290	0.198	**0.001**	0.131	**0.021**
EVI									
Estimate	-0.21	-0.02	0.77	-0.89	1.21	-0.08	-1.34	-0.23	-0.57
CI	-1.21, 0.79	-0.92, 0.87	-0.16, 1.70	-2.01, 0.24	0.23, 2.19	-1.04, 0.89	-2.42, -0.27	-1.24, 0.79	-1.49, 0.34
p	0.682	0.958	0.106	0.123	**0.016**	0.874	**0.015**	0.661	0.218
Random Effects									
σ^2	0.19	0.19	0.19	0.19	0.19	0.19	0.19	0.19	0.19
$\tau_{00\ Obs.\ Period}$	0.14	0.14	0.16	0.14	0.15	0.14	0.14	0.14	0.13
$_{Group}$	0.05	0.05	0.05	0.06	0.05	0.05	0.05	0.05	0.05
ICC	0.49	0.49	0.52	0.51	0.50	0.49	0.50	0.49	0.49
Groups	6	6	6	6	6	6	6	6	6
Obs. Periods	30	30	30	30	30	30	30	30	30
N	469	469	469	469	469	469	469	469	469
R^2_M	0.001	0	0.01	0.011	0.019	0	0.034	0.001	0.006
R^2_C	0.494	0.494	0.525	0.513	0.512	0.494	0.518	0.495	0.492
AICc	656.299	656.688	654.270	653.884	650.698	656.523	650.371	656.257	655.137

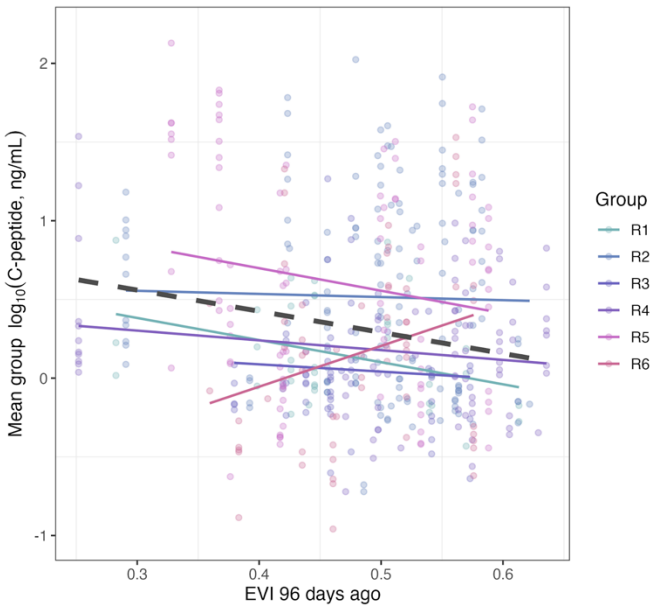


Figure 3.5. Energy balance with respect to EVI. Plot representing a linear mixed effect regression model of energy balance against EVI values from 96 days prior (dashed black line, *Period –6*). Energy balance is the group mean of $\log_{10}$-transformed urinary c-peptide values (UCP ng/sg) per day from urine samples from six red-tail groups. EVI values are aggregated 16-day MODIS Enhanced Vegetation Indices. Colored solid lines represent simple regressions of the EVI-C-peptide relationship per group.

Table 3.2. C-peptide model selection. Information-theoretic comparison of linear mixed-effect regression models (Burnham and Anderson 2002). N = 469 mean urinary c-peptide values per group per day, for all models. Only one model (model *Period –6*, the EVI period occurring six cycles prior to the current cycle; see Table 3.1) fell within the confidence set of best-fit models, indicated in bold font. This model is 18% better at predicting mean group c-peptide values than the next-best model (*Period –4*). Models are in descending order of predictive strength, indicated by their Akaike Information Criterion values corrected for small sample sizes (AICc), the difference from the strongest model (Δ_i), and their weight (ω_i). RSS is the residual sum of squares, and K indicates the number of model parameters.

Model	RSS	K	AICc	Δ_i	ω_i
Period –6	**83.2852**	**5**	**650.37**	**0.00**	**0.41**
Period –4	83.1985	5	650.70	0.33	0.35
Period –3	83.8408	5	653.88	3.51	0.07
Period –2	83.3457	5	654.27	3.90	0.06
Period –8	84.3918	5	655.14	4.77	0.04
Period –7	84.4946	5	656.26	5.89	0.02
Period 0	84.5296	5	656.30	5.93	0.02
Period –5	84.5453	5	656.52	6.15	0.02
Period –1	84.5468	5	656.69	6.32	0.02

biomass (Table 3.3B, *Period –2*; β = -6.91, CI = -10.93, -2.89, conditional R^2 = 0.758, p = 0.001), and with the amount of easily digestible sugars in the home range, measured in TNC (Table 3.3C, *Period –2*; β = -4.33, CI = -7.68, -0.99, conditional R^2 = 0.185, p = 0.012). There were no significant relationships between EVI and the quantity of ripe fruit (Table 3.3A), but the time lag of the strongest of its models (*Period –6*) corresponds to the time lag of the strongest model evaluating EVI as a predictor of UCP.

3.4 DISCUSSION

3.4.1 Energy Balance and Phenological Cycles

The findings from our study indicate significant correlations between EVI and both energy balance in red-tailed monkeys and fruit production in their habitat. The strong negative relationship between EVI values from 96 days prior and UCP levels suggests that lower EVI values, indicative of periods of leaf flushing, correlate with higher energy balance in red-tailed monkeys. This time lag aligns with the known phenological cycle in tropical rainforests, where leaf flushing often precedes fruiting by approximately 2.5 months, but can be up to 4 months in African rainforests (van Schaik & Pfannes, 2009). The strength of this model (*Period –6*) compared to others in this set (Table 3.1) emphasizes the critical role of accurately timing phenological events to better predict primate foraging behavior. However, while the model shows a significant relationship, the raw individual UCP data exhibit substantial scatter (Fig. 3.5), suggesting that EVI alone may not be a sufficient predictor of UCP. Although the direction of the relationship holds, the strength may not be robust enough to reliably predict UCP values across all time points.

Several assumptions may have influenced these results. First, the use of EVI as a proxy for fruit availability rests on the assumption that this particular vegetation index can capture

Table 3.3. VIs as predictors of fruit availability. Mixed-effect linear regression models of the relationship between Enhanced Vegetation Indices (EVI) and fruit availability. The phenology outcomes represent fruit availability measured within red-tailed monkey group home ranges every observation period and estimated using three measures: quantity (the estimated number of fruit; **A**), biomass (in Kg; **B**), and total non-structural carbohydrates (TNC, in g; **C**). The models evaluate EVI calculated for the current observation period (*Period 0*; Fig. 3.3) and extend backward sequentially in eight 16-day cycles (*Period –1* through *Period –8*) from the median day of each observation period. σ^2 = Mean random effects variance; τ_{00} = Random intercept variance: observation period, group; R^2_M = Marginal R^2; R^2_C = Conditional R^2; AICc = Akaike information criterion, adjusted for small sample sizes. Shaded gray columns denote the strongest model within each set.

A) Phenology - Quantity

	Period 0	Period -1	Period -2	Period -3	Period -4	Period -5	Period -6	Period -7	Period -8
Intercept									
Estimate	0.21	-0.54	0.51	-0.51	-0.57	-0.18	0.69	0.4	0.38
CI	-1.19, 1.61	-1.45, 0.37	-0.80, 1.81	-1.62, 0.60	-1.89, 0.76	-1.26, 0.91	-0.41, 1.79	-0.64, 1.44	-0.64, 1.40
p	0.766	0.236	0.440	0.361	0.396	0.747	0.215	0.447	0.465
EVI									
Estimate	-0.76	0.77	-1.34	0.68	0.8	0.02	-1.76	-1.14	-1.12
CI	-3.53, 2.01	-1.00, 2.53	-3.89, 1.21	-1.45, 2.81	-1.79, 3.39	-2.14, 2.18	-3.97, 0.45	-3.19, 0.90	-3.15, 0.91
p	0.587	0.388	0.298	0.526	0.541	0.986	0.117	0.268	0.274
Random Effects									
σ^2	0.15	0.14	0.15	0.14	0.15	0.15	0.15	0.15	0.14
$\tau_{00\ \text{Obs. Period}}$	0.27	0.27	0.26	0.27	0.26	0.27	0.25	0.25	0.29
$_{\text{Group}}$	0.03	0.04	0.03	0.05	0.04	0.04	0.02	0.03	0.04
ICC	0.67	0.69	0.66	0.68	0.67	0.68	0.64	0.65	0.70
N	66	66	66	66	66	66	66	66	66
R^2_M	0.006	0.011	0.024	0.006	0.006	0.000	0.051	0.022	0.019
R^2_C	0.676	0.689	0.668	0.686	0.676	0.677	0.659	0.657	0.704
AICc	121.541	121.982	120.968	121.979	121.602	122.312	120.101	121.27	121.292

B) Phenology – Biomass

	Period 0	Period -1	Period -2	Period -3	Period -4	Period -5	Period -6	Period -7	Period -8
Intercept									
Estimate	1.68	0.76	3.56	0.38	1.04	-0.28	-0.88	1.06	0.54
CI	-0.54, 3.90	-0.76, 2.28	1.51, 5.62	-1.45, 2.20	-1.16, 3.24	-2.08, 1.52	-2.72, 0.96	-0.66, 2.78	-1.18, 2.26
p	0.135	0.319	**0.001**	0.682	0.347	0.759	0.343	0.222	0.531
EVI									
Estimate	-3.20	-1.36	-6.91	-0.56	-1.89	0.77	2.01	-1.96	-0.92
CI	-7.61, 1.21	-4.34, 1.63	-10.93, -2.89	-4.10, 2.99	-6.22, 2.43	-2.84, 4.38	-1.69, 5.70	-5.37, 1.45	-4.38, 2.54
p	0.152	0.367	**0.001**	0.754	0.384	0.673	0.281	0.255	0.596
Random Effects									
σ^2	0.49	0.47	0.36	0.47	0.45	0.47	0.47	0.49	0.47
$\tau_{00\ Obs.\ Period}$	0.61	0.67	0.85	0.69	0.70	0.67	0.61	0.63	0.70
$_{Group}$	0.02	0.04	0.00	0.04	0.05	0.05	0.10	0.02	0.04
ICC	0.56	0.60	0.70	0.61	0.62	0.61	0.60	0.57	0.61
N	66	66	66	66	66	66	66	66	66
R^2_M	0.042	0.014	0.193	0.002	0.013	0.004	0.025	0.025	0.005
R^2_C	0.580	0.609	0.758	0.609	0.628	0.607	0.611	0.580	0.615
AICc	187.235	188.988	180.173	189.38	188.314	189.254	188.448	188.453	189.244

C) Phenology - TNC

	Period 0	Period -1	Period -2	Period -3	Period -4	Period -5	Period -6	Period -7	Period -8
Intercept									
Estimate	2.34	0.98	2.29	0.29	0.57	-0.64	-1.48	1.55	0.29
CI	0.34, 4.34	-0.48, 2.44	0.55, 4.04	-1.50, 2.07	-1.53, 2.67	-2.22, 0.93	-3.00, 0.04	-0.01, 3.11	-1.37, 1.95
p	**0.023**	0.184	**0.011**	0.750	0.588	0.418	0.057	0.051	0.732
EVI									
Estimate	-4.49	-1.80	-4.33	-0.40	-0.98	1.49	3.27	-3.01	-0.42
CI	-8.43, -0.56	-4.66, 1.05	-7.68, -0.99	-3.86, 3.05	-5.13, 3.17	-1.65, 4.63	0.20, 6.34	-6.13, 0.12	-3.74, 2.91
p	**0.026**	0.211	**0.012**	0.816	0.638	0.345	**0.037**	0.059	0.803
Random Effects									
σ^2	1.00	1.05	0.95	1.07	1.06	1.04	0.97	1.05	1.07
$\tau_{00\ Group}$	0.06	0.07	0.10	0.09	0.09	0.12	0.15	0.02	0.09
ICC	0.05	0.06	0.10	0.08	0.08	0.11	0.14	0.02	0.08
N	62	62	62	62	62	62	62	62	62
R^2_M	0.078	0.026	0.099	0.001	0.004	0.013	0.063	0.058	0.001
R^2_C	0.127	0.083	0.185	0.078	0.083	0.118	0.189	0.077	0.079
AICc	183.867	187.955	182.695	189.056	188.515	188.419	185.057	186.286	189.123

relevant aspects of the foraging landscape (Gray & Ewers, 2021), such as the timing of leaf flushing (i.e., EVI minimum). EVI primarily reflects vegetative greenness, and despite the presumed lag between leaf flushing and fruiting, it may not directly correspond to the nutritional quality or abundance of fruiting bodies, which should directly influence increases in energy balance. In particular, the relatively low seasonal variation in maximum temperature in the tropics (Fig. S3.1) causes tropical plants to be sensitive to sudden and sharp temperature changes, which can result in crop failure through several pathways (e.g., dysregulation of flowering or under-development of fruit; Slot & Winter, 2016). Including temperature as an additional variable in the models could account for such effects and potentially draw a stronger connection between the size of trees, the maturity of their leaves, and the amount of fruit produced. The scatter in the data might also reflect inter-individual variation in energy balance, other unmeasured environmental factors (e.g., temperature), or physiological variables (e.g., reproduction or energetic tradeoffs, see Chapter 4), as well as interspecific interactions (see Chapter 2), which could affect energy balance independent of fruit availability.

In addition to its correlation with UCP, EVI from 32 days prior also had a strong negative relationship with the biomass of ripe fruit and the amount of easily digestible sugars (TNC) in the home range. This finding indicates that EVI can serve as a predictor for the availability of crucial food resources for frugivorous primates. Primatologists use many methods to assess fruit availability, but most include a human-monitored visual estimate of crop size and have notable limitations (Marshall & Wich, 2013). While in this study, EVI was effective in predicting the overall biomass and quality of available fruit, its lack of significant

correlation with the quantity of fruit supports the need for more integrative approaches in studies of primate feeding ecology.

This distinction is critical because feeding behavior is strongly influenced by the nutritional content of fruit rather than the mere presence of fruit in a habitat (Raubenheimer et al., 2009). However, many studies still rely solely on visual counts to estimate fruit availability. The observed correlation between EVI and biomass and TNC reinforces the value of EVI in understanding the nutritional landscape that primates navigate. To improve the overall fit of phenology models, incorporating additional environmental variables such as rainfall, temperature, and irradiance—known correlates of fruit production (Potts et al., 2020)—could provide a more comprehensive understanding of variations in fruit availability. Furthermore, EVI values are likely influenced most by large trees that dominate the canopy within each home range, but these may not be key components of the red-tail diet. Evaluating changes in EVI as a predictor of phenological measures for specific species might yield a more accurate relationship between this remote-sensed vegetation index, the quality and productivity of each red-tail group's home range, and individual energy gain.

Evaluating EVI in combination with environmental variables and plant species that are important in the red-tail diet could yield a more holistic picture of the environmental factors influencing primate foraging behavior and resulting patterns of energy gain. Finally, physiological factors, such as hormonal stress markers or metabolic rates, could be integrated into future models to account for variation in UCP that may not be explained by environmental factors alone. This could help clarify the conditions under which UCP is more closely tied to fruit availability, as well as the periods where other physiological demands may dominate.

3.4.2 Primate Behavior and Life History

The use of UCP as a measure of energy balance provides a valuable proxy for more traditional, labor-intensive methods of tracking primate foraging patterns. While red-tail energy balance does not correlate with traditional estimates of fruit abundance (Table S3.4 in Chapter 2), it does correspond with EVI, which has implications for our understanding of their life history. Red-tailed monkeys reproduce year-round, but most births occur from January-March (Cords, 1984), coinciding with the dry season (Fig. S3.2). The latter part of their six-month pregnancy overlaps with the long wet season, between September and November, when EVI is the highest. This period aligns with the highest UCP values throughout the year (Fig. S2.1 in Chapter 2). These observations suggest that red-tails align more with the capital breeding end of the life history spectrum (Emery Thompson, 2013; Drent & Daan, 1980) and rely on accumulating sufficient energy reserves during the wet season to support the energetically demanding period of lactation during the dry season. It is unclear why red-tails give birth during a period of food scarcity (EVI minima; Fig. S3.2), but perhaps these energy demands are offset by other physiological constraints, such as thermoregulation (see Chapter 4). This approach highlights the potential of combining remote-sensed data with biomarker analysis to gain insights into primate behavior and energetics.

3.4.3 Implications for Conservation and Future Research

Our results have several implications for the study of frugivorous primates and their conservation. The strong and lagged correlation between EVI and energy balance emphasizes the importance of evaluating habitat characteristics at time scales other than the immediate present, allowing for the identification of critical periods of food scarcity and

areas of high biodiversity value. Determining the periodicity of ecological interactions often occurs after fieldwork has concluded, and using remote-sensed and publicly available data provides a means to expand the spatial and temporal monitoring capabilities of a single research group. Using EVI to monitor phenological changes offers a cost-effective and comprehensive method for assessing food availability, which is crucial for primate conservation, helping primatologists overcome barriers that prevent in-depth research on many species. The vast majority of primatological research focuses on just a handful of species (Bezanson & McNamara, 2019), leaving hundreds of primate species lacking *in-situ* data, which severely limits the effectiveness of conservation efforts. Long-term monitoring using EVI can bridge this gap by providing easily accessible and highly valuable data for developing adaptive conservation strategies. This method can help identify critical periods of food scarcity (Axel et al., 2024), areas of high biodiversity value (Silveira et al., 2021), and inform conservation strategies to mitigate the impacts of environmental changes.

Lastly, EVI can help track the impacts of climate change and habitat degradation on phenological cycles and primate populations, and combining it with other environmental variables, such as precipitation or temperature (e.g., Coops et al., 2018), could provide a more holistic understanding of the broader environmental factors influencing primate foraging behavior. To our knowledge, this is the first study to test the use of EVI as an indicator of fruit availability for frugivorous, arboreal primates in tropical rainforests. Future studies might consider exploring the application of EVI to studies of different primate species and habitats to validate its effectiveness as a universal predictor of fruit availability and energy balance.

3.5 CONCLUSION

The diversity of diets and complexity of rainforest ecosystems demand a multifaceted approach to understanding how different species access and use available food sources. Our study provides strong evidence that EVI is a valuable tool for predicting fruit availability and energy balance in frugivorous primates in tropical rainforests. By correlating EVI values with a biomarker of physical condition and on-the-ground observations of fruit production, we demonstrated that remote-sensed data could effectively reflect the nutritional landscape these primates navigate. Integrating satellite-based VIs with ground observations offers a promising avenue for more accurate assessments of fruit availability. However, variability in phenological responses and environmental influences highlight the challenges in conserving and managing primate populations sustainably. Our study underscores the transformative potential of combining remote sensing technology with ecological and behavioral research, paving the way for more nuanced and effective conservation efforts in dynamic rainforest ecosystems.

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IV. The Energetic and Reproductive Costs of Between-Species Competition

4.1 Introduction

Like dark matter in the universe, between-species feeding competition exists nearly everywhere in nature, is hard to detect, and exerts substantial pressure on the entities in its reach (Begon et al., 1996; Connell, 1983). Competition between species has the potential to constrain individual reproduction and population size (Grether et al., 2017; Watts & Holekamp, 2008; Yunger et al., 2002) and plays a substantial role in community structure and stability, even affecting the dynamics of social interactions within a species (Carrete et al., 2010). Most primates live in highly speciose communities that present the potential for strong between-species competition for food resources (Fleagle et al., 1999; Schreier et al., 2009). This competition should most strongly affect the smallest primates, whose physiological demands–higher metabolic rates and energy needs– make them particularly vulnerable to the energetic costs of competition (Gaulin, 1979; Kleiber, 1947). Yet small, arboreal primates are the subject of far less research than large-bodied species (like apes) or those living in more open, non-rainforest environments with fewer competing primate species (like macaques, vervets, and baboons; Titley et al., 2017; Troudet et al., 2017). As a result, it is unclear how the energetic shortfalls associated with competition influence reproduction, which can affect life-long outcomes in small primates. I address these unknowns by asking: how does between-species competition affect energetic condition and fitness? Clarifying the effect of interspecific competition on individual reproductive outcomes and identifying its role in population dynamics can help improve the management

and conservation of primate populations (Guillaumet & Russell, 2022; Wang et al., 2024), most of which are in decline or are threatened with extinction (Estrada et al., 2017).

I investigate how natural variation in community composition leads to varying energetic outcomes for a small-bodied primate using red-tailed monkeys (*Cercopithecus ascanius*) – the smallest diurnal, arboreal, fruit-eating primate in the rainforests of Eastern Africa – at three locations that differ in their primate community composition. I measure the relationship between competitive pressure and red-tailed monkey physical condition at these sites to assess the overall strength of between-species feeding competition. To link competitive pressure to individual fitness, I examine variation in short-term reproductive success as a consequence of competition.

4.1.1 Between-Species Competition

Competition for limited food resources is widespread, and its intensity and variability shape the patterning of social relationships (Janson & van Schaik, 1988; Koenig, 2002), life history traits (Harris & Siefferman, 2014; Sanders & Gordon, 2000), and population demography (Peres & Dolman, 2000). Ecological communities are groups of interacting species that live in the same place and are characterized by a web of competitive pressures that they exert on each other (Reed & Bidner, 2004; Strong Jr et al., 2014), but it is feeding guilds – i.e., sets of species that exploit the same resources – that likely impose the strongest costs on each other (Simberloff & Dayan, 1991). Though competition for limited resources is common in animal communities, it is notoriously challenging to measure because of the counter-strategies individuals employ to reduce the frequency and intensity of direct conflicts (Chesson, 2000). Consequently, decades of primatological research have focused on feeding competition within species (i.e., intraspecific competition), with far less attention on

competition between species (Eckardt & Zuberbühler, 2004; Lambert, 2012; Palm et al., 1986), particularly among those within the same feeding guild.

While absolute body size determines an animal's energetic requirements and influences its dietary constraints (Gaulin, 1979; Kleiber, 1947), relative body size shapes how it exerts and responds to competitive pressure from other species (Alatalo & Moreno, 1987; Basset & L. Angelis, 2007; Moreno-Opo et al., 2020; Woodward & Hildrew, 2002). For instance, larger animals monopolize feeding sites by evicting smaller animals (Houle et al., 2014; Thiel et al., 2021). Smaller animals, which usually occur at higher densities and move within smaller areas, tend to rapidly find and exploit resources before the arrival of larger competitors. As a result, both large and small species suffer from the depletion of food by others (referred to as exploitation or scramble competition; Birch, 1957; Putman & Putman, 1994). However, smaller species also suffer directly from agonistic encounters with larger, more dominant species (interference or contest competition). Thus, small species likely experience larger cumulative energetic costs of competition than larger species. Small primates also face different physiological pressures: the larger ratio of surface area to volume requires them to expend more energy relative to their body size than larger animals (Kleiber, 1947), demanding diets that are relatively higher in energetic and nutritional content (Gaulin, 1979; McGrosky & Pontzer, 2023). Coupled with more intense competition, the need to find and consume high-quality food creates greater energetic constraints for small primates, a force shaping nearly every evolved aspect of their behavior and life history (Sibly & Brown, 2007; Speakman, 1997). Assessing the energetic consequences of competition is therefore imperative for building a better understanding of the strategies that smaller primates use to coexist among numerous larger competitors.

Throughout the rainforests of Eastern Africa, several primate species routinely coexist and share highly similar, *fruit-based diets*: the red-tailed monkey (*Cercopithecus ascanius*; male/female mass = 4/3 kg), blue monkey (*C. mitis*; 7/4 kg), grey-cheeked mangabey (*Lophocebus albigena*; 9/6 kg), and chimpanzee (*Pan troglodytes*; 43/35 kg; Bryer et al., 2013; Conklin-Brittain et al., 1998; Houle et al., 2006; Struhsaker, 1978). The three monkey species often travel and feed in close proximity (Bryer et al., 2013; Struhsaker, 1981; Chapter 2 of this dissertation), increasing the chances of direct competitive interactions, and their diets overlap with each other and with chimpanzees more than with other, non-primate competitors (Conklin-Brittain et al., 1998, 1998; Houle et al., 2006; Raubenheimer et al., 2015). A *size-based hierarchy* among these species determines their access to preferred fruits (Houle et al., 2010; Waser & Case, 1981). At the top of the hierarchy, the chimpanzee diet closely mirrors the availability of their preferred foods; i.e., as ripe fruit increases in abundance, chimpanzees consume more fruit (Watts et al., 2012a, 2012b) and exhibit better physical condition (Emery Thompson et al., 2009; Sherry & Ellison, 2007). This pattern does not hold for red-tailed monkeys (Chapter 2; Steinitz et al., *in prep*), which are at the bottom of the size hierarchy (Houle et al., 2010). Due to the risk of predation by chimpanzees, red-tails actively avoid them as they navigate their *"landscape of fear"* (Laundré et al., 2010). At the Ngogo Research Station in Kibale National Park, Uganda, red-tails occupy small home ranges (~0.35 km^2; Chapter 2) within the much larger chimpanzee range (~35 km^2, circa 2012; Mitani et al., 2010; Fig. 2.2a in Chapter 2), and the presence of chimpanzees within a red-tail home range fluctuates with the availability of ripe fruits (Chapter 2; Steinitz et al., *in prep*). Red-tail energetic condition exhibits the expected pattern, a positive correlation with the abundance of important fruits, only when chimpanzees are absent from the red-tail home range (Fig. 2.2c in Chapter 2). As preferred foods for chimpanzees become more

abundant, chimpanzees spend increasingly more time foraging within the red-tail range, obstructing the red-tails' access to food. As a result, red-tail energetic condition declines, and the correlation between fruit abundance and energy gain reverses. This pattern demonstrates the strong effect that between-species competition can have on the ability of small-bodied consumers to profit from local resources.

However, this competitive pressure may not be universal, and other large-bodied competitors might not have the same effect on red-tailed monkeys. Grey-cheeked mangabeys are food competitors with red-tailed monkeys, but red-tails actively pursue associations with them (Bryer et al., 2013; Struhsaker, 1981; Chapter 2), likely because mangabeys provide protection from aerial predators (Arlet & Isbell, 2009; Wrangham et al., 1996). Red-tails at Ngogo form close-range associations with mangabeys up to 83.5% of the time (Chapter 2), compared to only up to 31.6% with blue monkeys. Associations with mangabeys result in decreased energy gain in red-tails (Table S4 of Chapter 2), while blue monkeys do not affect them. These differences suggest that the benefits and costs of polyspecific associations vary based on the species involved. As intraguild predators, (Amarasekare, 2008; Holt & Polis, 1997), and due to their body size, dominance, and predatory behavior, the cost exerted by chimpanzees is even higher than that of mangabeys (Table S4 in Chapter 2). The Ngogo chimpanzee community is exceptionally large (circa 2013; Langergraber et al., 2013; Watts, 2018) and over triple in density (kg per km^2; Brown & Waser, 2018) than other communities within the same forest, which makes the risk of encountering a chimpanzee particularly high for red-tails at this site. It remains to be tested whether the extreme effect that chimpanzees have on red-tails is specific to their role as both competitors and predators (Bleicher, 2017; Coleman & Hill, 2014) rather than a general

characteristic of feeding competition from larger competitors. I test this idea by studying the physical condition of red-tailed monkeys at several sites with different sets of competitors.

4.1.2 Consequences of Competition

Feeding competition should shape short-term patterns of energy gain (Brown et al., 2022; Emery Thompson, 2017), which ultimately shape long-term patterns of investment in reproduction (Emery Thompson et al., 2012b). The relationship between food and reproductive success is widely observed across species (vertebrates: Boutin, 1990; cotton rats: Doonan & Slade, 1995; birds: Lack, 1947; snowshoe hares: O'donoghue & Krebs, 1992; red squirrels: Wauters & Lens, 1995). However, the number of red-tailed monkey infants born does not correspond with fluctuations in food availability (Rode et al., 2006), suggesting a surprising disconnect between food availability and fitness outcomes. Previous attempts to estimate the energetic costs of between-species interactions have mainly been conducted in the lab or in outdoor cages and focus heavily on the costs of predation risk (e.g., Abrahams & Dill, 1989; Nonacs & Dill, 1990). The energetic costs of *intraspecific* feeding competition were assessed in white-faced capuchins (*Cebus imitator*) using non-invasive measures of physical condition, and indicate that periods of intense within-group competition have a negative effect on physical condition (Bergstrom et al., 2020). However, within-group rank hierarchies did not shape patterns of energy gain, either because fallback foods might allow low-ranking individuals to match equity with higher-ranking ones, or because there are other, extrinsic pressures that have yet to be evaluated. Of the existing studies on primate ecological guilds, none address the effect of interspecific feeding competition on the energetic condition or reproductive outcomes of sympatric species (Almeida-Silva et al., 2005; Chivers, 1998; Dammhahn & Kappeler, 2014; Falótico et al.,

2021; Gautier-Hion, 1980; Hladik, 1977; Houle et al., 2006; Kamilar & Ledogar, 2011; Struhsaker, 1978; Struhsaker & Oates, 1975; Terborgh, 2014; Thiel et al., 2021; Waser & Case, 1981). Thus, there is a critical need to determine how between-species competitive dynamics shape short-term fluctuations in energetic condition and any resulting reproductive effects.

4.1.3 Estimating Energetic Condition

Estimating an animal's energetic condition requires measuring energetic input (the amount of food consumed and the metabolic uptake of its nutrients), and energy expenditure (e.g., on basal metabolism and physical activity). The net difference between energy inputs and outputs is referred to as *energy balance* (Emery Thompson et al., 2009; Knott, 2001; Lee, 1987; Wade et al., 1996) and is the amount of energy available for allocation to metabolic demands, such as growth, reproduction, and mountain immune defenses (Emery Thompson et al., 2012b; Emery Thompson, 2013), a metric that changes over the course of hours as food is digested. Representing slightly longer time scales, *energy status* is the quantity of stored energy in fat reserves (Emery Thompson, 2017; Pontzer, 2015). These two components of physical condition are connected because over time, consistently positive energy balance results in added energy storage, and persistently negative energy balance leads to depleted stored energy. More broadly, physical condition can be generally categorized into states of energy gain (energy in > energy out; Fig. 4.1), neutrality (in ≈ out), mild to moderate energy loss (in < out), and severe, prolonged energy loss (in << out). Recent developments in the application of field-friendly preservation techniques for urine and fecal samples led to rapid proliferation in the use of non-invasive hormone assays,

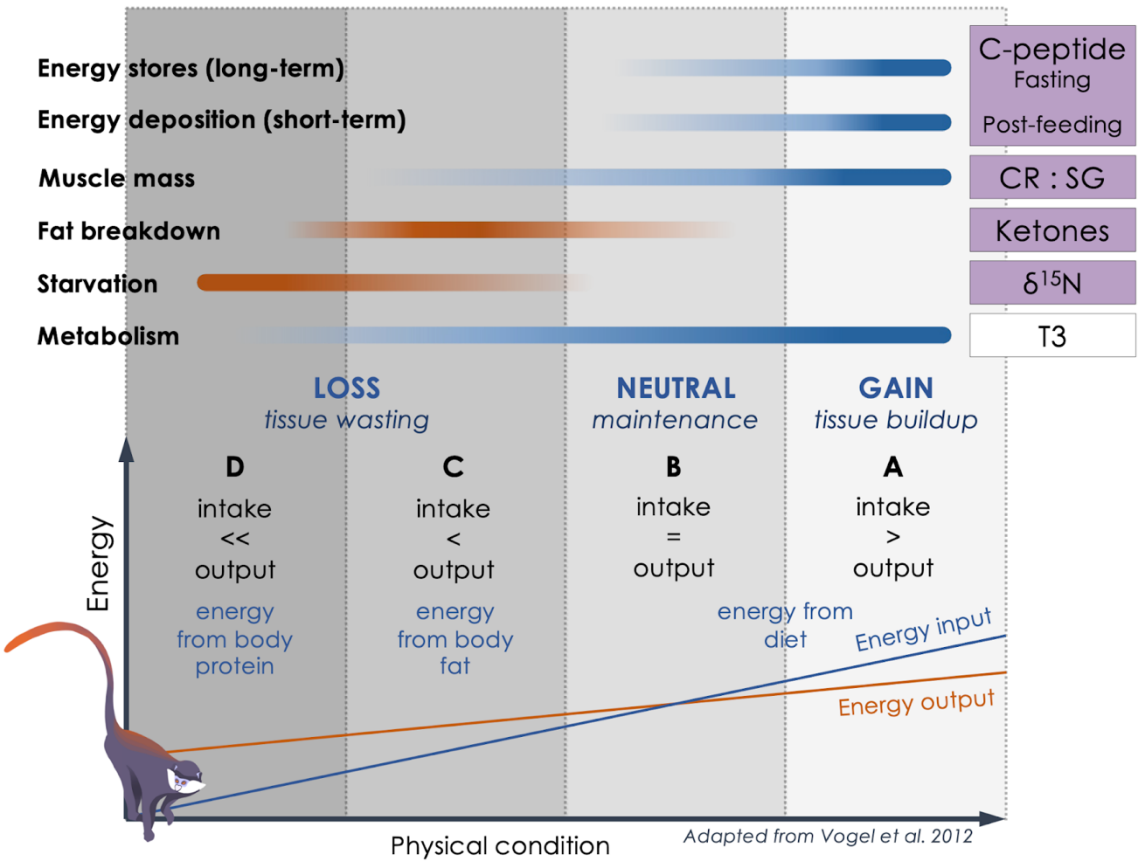

Figure 4.1. Theoretical Energy Mobilization Model (adapted from Vogel et al., 2012). An individual is in positive energy balance when energy intake exceeds energy output (**A**). As fruit availability declines, the individual transitions into a neutral physical condition (**B**). When energy intake is less than output, the individual begins to exhibit a decline in physical condition as a result of the breakdown of energy from fat stores (**C**). When these reserves are critically low, an individual transitions into an excessive energetic deficit, and glucose is liberated as body protein (muscles) catabolism via gluconeogenesis (**D**). Text boxes indicate the biomarkers (purple = urine; white = fecal), and the colored line gradients indicate the relative biomarker levels for each physical condition (A-D), with color intensity indicating increasing values (intense = high; transparent = low values).

and provide a means of identifying energetic condition in wild and unrestrained non-human primates (Behringer & Deschner, 2017).

Biomarkers are naturally occurring substances in the body that are used to estimate investment in underlying bodily functions. For example, insulin, a metabolic hormone, is

released by the pancreas to facilitate energy mobilization and the storage of surplus energy as fat, and its levels surge in response to circulating glucose while baseline levels indicate patterns of weight gain or loss (Deschner et al., 2008; Foster & McGarry, 1992; Sherry & Ellison, 2007). C-peptide is a by-product of insulin production that is immediately excreted in urine and easily assayed (Brown et al., 2022; Emery Thompson & Knott, 2008; Harris et al., 2010; Harrison et al., 2010). Fasting values of urinary C-peptide (UCP), such as those from first morning voids occurring before feeding, indicate whether an animal is gaining or losing weight, while post-feeding measures indicate short-term surges of insulin in response to glucose from food (Box 4.1; Girard-Buttoz et al., 2011). Individuals who are gaining weight can have fasting UCP values that are 2-6 times higher than those who are losing weight (Deschner et al., 2008; Emery Thompson & Knott, 2008; Girard-Buttoz et al., 2011). High values in fasting samples, relative to annual averages, demonstrate that an individual is gaining weight (condition A in Fig. 4.1), and lower values correspond with worse physical condition (conditions B-D).

While UCP values are useful for indicating periods of energy gain (condition A in Fig. 4.1), they do not distinguish among the other energy conditions, which necessitates the use of additional, non-invasively sampled biomarkers. The residuals of urinary creatinine and specific gravity (CR:SG) indicate relative muscle mass (Emery Thompson et al., 2012a). Creatinine is found primarily in muscle tissue and is excreted into urine at constant rates (Heymsfield et al., 1983). Individuals with higher muscle mass have higher absolute values of creatinine. The residuals from a regression of creatinine against specific gravity, an indicator of urine concentration, provide an estimate of muscle mass relative to body weight (i.e., below or above population slopes), a measure of leanness (Emery Thompson et al., 2012a). Low CR:SG values indicate an animal has lost muscle mass (conditions C and D). Ketone

bodies (hereafter, Ketones) are produced when adipose cells (fat reserves) are broken down for use as fuel and indicate that an individual is in negative energy balance (condition C; Knott, 1998; Robinson & Williamson, 1980).

Physical condition is dependent not only on food intake, but also on the amount of energy expended, the largest contributor to which is basal metabolism (Westerterp & Speakman, 2008). Triiodothyronine (T3) is an indicator of metabolic rate and is particularly responsive to nutritional deficits, during which it reduces metabolism and promotes energy conservation (Emery Thompson, 2017; Wasser et al., 2010). T3 increases during periods of energy surplus to mobilize energy toward tissue buildup (condition A). Stable nitrogen isotope ($\delta^{15}N$) values provide insights into the nutritional state and protein metabolism of individuals (Ben-David & Flaherty, 2012). In ecological and nutritional studies, $\delta^{15}N$ values are used to infer trophic levels and dietary sources. The ratio of the heavier to the lighter isotope (^{15}N:^{14}N) becomes progressively enriched in consumers, relative to their diet, due to the preferential excretion of the lighter isotope and the retention of the heavier isotope during protein metabolism and assimilation, a process known as isotopic fractionation. As a result, the higher an animal is in the food chain (for example, a carnivore compared to its herbivorous prey), the higher its $\delta^{15}N$ values. During starvation or severe undernutrition, when fat reserves are critically low, $\delta^{15}N$ values increase due to the catabolism of body proteins via gluconeogenesis, which becomes a significant source of nitrogen when dietary intake is insufficient (Hülsemann et al., 2017; Mekota et al., 2009; Vogel et al., 2012). The process involves recycling nitrogen from metabolic amino acid pools and preferentially retaining the heavier isotope, ^{15}N, in body tissues. As a result, during periods of severe undernutrition, the $\delta^{15}N$ values in body tissues become elevated compared to periods of

adequate nutrition (condition D). This enrichment reflects increased reliance on endogenous protein stores as a source of energy and nutrients (Mekota et al., 2009).

Box 4.1. Biomarker Panel. Table summarizing the biomarkers used in this study, their physiological roles, how they respond during energetic deficits, and the mean ± SD values from this study.

Biomarker	**Physiological indication**	**Change during energetic deficit**	**Mean ± SD in this study (min, max)**	**References**
C-peptide (UCP) corrected by specific gravity	A by-product of insulin production, excreted in urine, indicating circulating insulin levels and energy balance.	Fasting and post-feeding levels decrease, indicating reduced insulin production; if prolonged, results in weight loss.	9.95 ± 23.03 (0, 240.42) *ng/mL*[a]	Brown et al., 2022; Emery Thompson & Knott, 2008; Harris et al., 2010; Harrison et al., 2010; Girard-Buttoz et al., 2011; Steinitz et al., *in prep*
Creatinine residuals against specific gravity (CR:SG)	Indicate relative muscle mass and leanness.	Decreases as muscle mass is lost.	0.00 ± 0.31 (-0.75, 1.84) *residuals*[b]	Emery Thompson et al., 2012a; Heymsfield et al., 1983
Ketones corrected by specific gravity	Produced when fat reserves are used for fuel, indicating negative energy balance.	Increases as the body relies on fat stores for energy.	1.00 ± 4.30 (0.00, 38.19) *mM/mL*[a]	Knott, 1998; Robinson & Williamson, 1980
Triiodothyronine (T3)	Indicates metabolic rate.	Levels decrease to lower metabolic rate and conserve energy.	15.38 ± 8.90 (2.77, 58.53) *ng/dL*	Emery Thompson, 2017; Wasser et al., 2010
Stable Isotope ^{15}N ($\delta^{15}N$)	Indicates catabolism of body tissues.	Increases during starvation.	4.38 ± 1.54 (-3.51, 6.59) *‰*	Sandberg et al., 2012; Vogel et al., 2012

[a] UCP and Ketones are corrected by specific gravity (sg), a measure of urine concentration, to account for variations in urine concentration across samples (Miller et al., 2004).

[b] Creatinine is reported as the residuals from a regression of urinary creatinine against the sample's specific gravity (Emery Thompson et al., 2012a)

A biomarker panel has the additional benefit of elucidating patterns of energy gain across multiple time scales: whereas values of post-feeding UCP indicate short-term surges in energy due to daily feeding (Girard-Buttoz et al., 2011), composite values from the biomarker panel indicate longer-term changes in fat stores and other tissues (creatinine: Emery Thompson et al., 2012a; ketones: Robinson & Williamson, 1980; T3: Cristóbal-Azkarate et al., 2016; fasting UCP: Girard-Buttoz et al., 2011). Higher UCP and T3 reflect a positive energy balance, indicating that energy intake exceeds expenditure (condition A in Fig. 4.1). Prolonged periods of energy gain should correspond with increased CR:SG, indicating an increase in muscle mass. When CR:SG remains stable, but UCP is low, and T3 increases, energy intake is roughly equal to expenditure, potentially indicating muscle maintenance without significant surplus (condition B). Similarly, low ketone levels or their absence - while UCP remains stable - also indicates that animals are gaining short-term energy, but overall energy intake is intermediate, and the animal is not gaining sufficient energy to increase fat stores (condition B). A negative energy balance (condition C) should correspond with lower UCP and higher ketones, indicating a reliance on fat reserves, and a lower T3 for energy conservation. A more severe and prolonged energy deficit (condition D) is evident when CR:SG and UCP are low and $\delta^{15}N$ is high, indicating significant nutritional stress, critically low fat reserves, and a metabolic shift to catabolism of muscle protein. In this condition, low T3 would reflect a prolonged state of energy conservation. However, contradicting patterns might emerge; individuals can have a high energy status (significant fat stores) while simultaneously being in negative energy balance (losing weight), a state common among primates in seasonal habitats (Emery Thompson, 2017). In addition, these conditions might highlight periods where access to resources departs from patterns of food

availability, resulting from strong competition or other environmental constraints that create exceptional metabolic stress.

4.1.4 Fitness Consequences of Competition

Between-species feeding competition may also exert longer-term effects on small-bodied primates. Unlike other animals, which can adjust their litter size when experiencing caloric limitation, reproduction presents a greater challenge for Anthropoid primates, which usually produce a single dependent offspring at a time (Chapman, 1990). Consequently, when female primates have insufficient access to energy resources, they have longer inter-birth intervals (Ellison, 2003; Emery Thompson et al., 2012b; Emery Thompson & Wrangham, 2008). Competitive pressures strong enough to exclude primates from limiting resources are also likely to limit individual fitness. However, primates have long lifespans, and it would take decades to fully document and contrast these fitness measures. Instead, I propose an intermediate test: short-term evaluation of group-wide reproductive productivity. Investment in reproduction should be higher in groups experiencing less competition, and periods of energy shortfall should be characterized by lower reproduction within the group.

4.2 Hypotheses and Predictions

The outstanding question addressed here is whether the energetic effects of feeding competition from multiple species are cumulative. One possibility is that the extent of *energetic suppression* experienced by red-tails is a function of the number of larger-bodied competing species (**H1: *Additive Effects***; Fig. 4.2b, c; Prins & Olff, 1998). If true, then red-tailed monkeys should exhibit a stronger positive relationship between energy balance and fruit abundance at sites with fewer competitors, compared to sites with more competitors

(P1a). The physical condition of red-tails in a competitor-free environment will depend primarily on food availability, whereas for red-tails in competitor-dense environments, physical condition will be a function of the number of competing species (Fig. 4.2b, c; P1b). Moreover, because chimpanzees are predators of red-tailed monkeys, they are expected to be the only competitor to cause the complete reversal of the food-energy relationship for red-tails (P1c). By extension, the effect that competitors have on food-energy patterns should

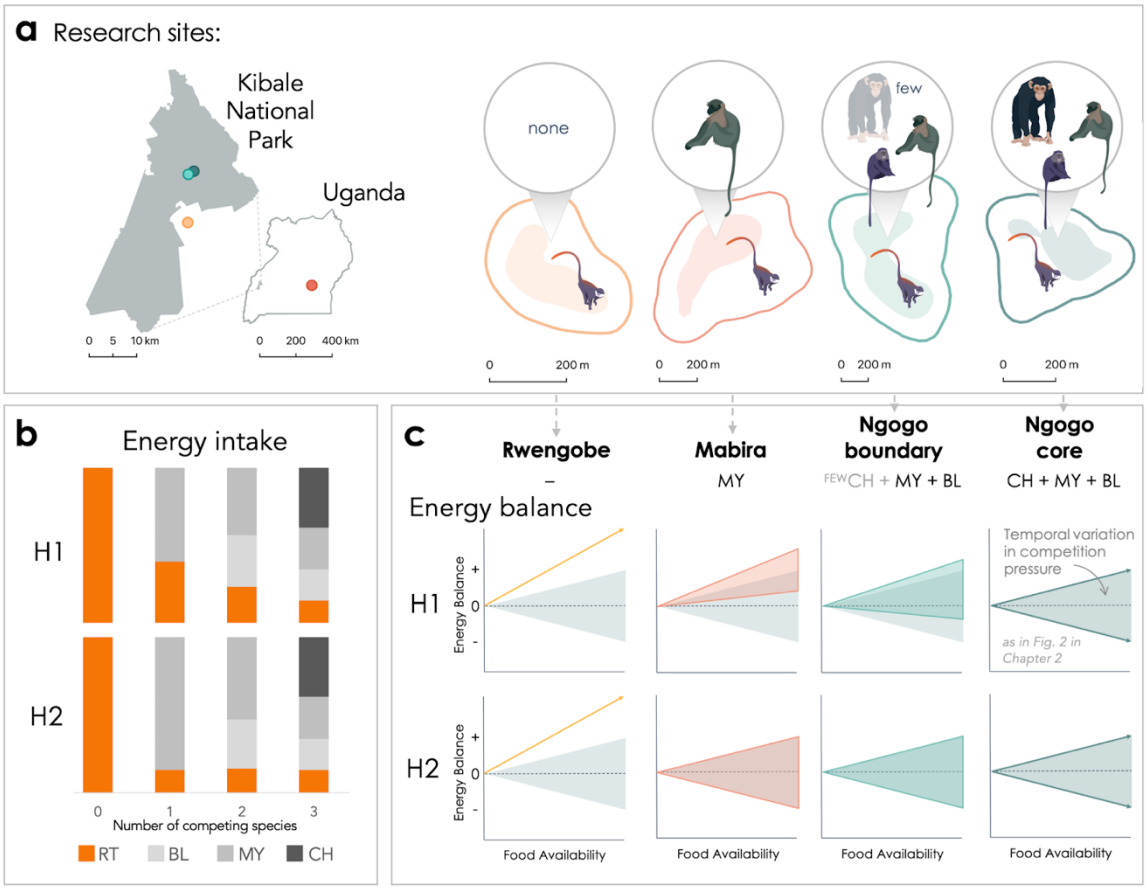

Figure 4.2. Research Sites, Hypotheses, and Predictions. a) Research sites with different primate community compositions. Polygon lines and dark centers indicate red-tailed monkey group home ranges (95% and 50% kernel density estimates, respectively) calculated using group center of mass coordinates logged every 30 minutes during group follows. **b) Hypotheses:** two alternative hypotheses of red-tail energy intake in competitor-dense environments. Barcharts illustrate the energy intake of red-tailed monkeys (orange) relative to other species in their habitat, with respect to the number of competing species

ranging from 0 to 3. Shades of grey depict the energy intake of the competing species, blue monkeys (BL), grey-cheeked mangabeys (MY), and chimpanzees (CH). These hypothetical energy intake models correspond to the research sites in this study: Rwengobe, with no competitors; Mabira, with MY only; Ngogo boundary, with BL and MY and few chimpanzees; and Ngogo core, with BL, MY, and CH. **H1** depicts the *additive effects* of competition; red-tails show a stronger positive correlation between energy balance and fruit abundance in environments with fewer competitors, with physical condition being influenced primarily by fruit availability in competitor-free areas. Alternatively, **H2** depicts the *universal effects* of competition; red-tails are equally suppressed regardless of the species and number of competitors, and energy intake depends on the carrying capacity of the environment. **c) Predictions:** theoretical model of the variation in red-tailed monkey energy gain as a function of fruit availability and the number of competing species. The pale background triangle in each plot represents the range of relationships between fruit availability and energy balance seen at Ngogo as a function of feeding competition from chimpanzees (Fig. 2.2 in Chapter 2). The superimposed arrows and triangles indicate the relationships predicted by the two hypotheses. H1: an increasing number of larger competing species introduces greater variance in the relationship between fruit availability and energy gain for red-tailed monkeys. H2: the presence of 1, 2, or 3 competing species has the same effect on red-tailed monkey energy gain, compared to red-tails living without competitors.

affect red-tail reproduction, creating a negative relationship between reproductive productivity and the number of competing species (P1d).

In contrast with these predictions, I observed a different pattern during a pilot study that I conducted from June through August 2019. I studied four groups of red-tailed monkeys across various locations in Uganda (Fig. 4.2a; see *4.3.2 Study Sites*). The Rwengobe group, which experiences no feeding competition from other arboreal frugivorous primates, showed higher adjusted UCP levels compared to groups coexisting with competitors (Fig. S4.1). Despite varying numbers of competing species across the other groups, the red-tails exhibited similar energetic conditions, indicating that each group may be in an environment at carrying capacity, where any degree of competition equally suppresses the smallest consumers. Surprisingly, mangabeys appeared to suppress red-tails as much as predatory chimpanzees. These findings suggest that further research is needed to confirm this pattern.

Based on these early results, I propose an alternate hypothesis: i.e., that larger-bodied food competitors have a universal effect on smaller consumers, regardless of whether the top competitor is a predatory chimpanzee or a protective grey-cheeked mangabey (**H2: *Universal Effects***; Fig. S4.1). In this case, I predict that the relationships between food availability and red-tail energy balance will look similar at any site with at least one larger-bodied competing species present (P2a). In other words, there is a positive relationship between food abundance and energy gain for the smaller species when the larger competitor is absent from the smaller species' home range; however, this relationship becomes negative when the larger competitor uses the home range of the smaller species extensively (as in Fig. 2.2 and Table S2.4 in Chapter 2). By extension, smaller consumers should spend less time in a condition of energy gain (condition A in Fig. 4.1) at sites with competitors compared to a site without competitors (P2b), and we should see the same reversal of the food-energy relationship at sites with any number of competitors (P2c). Lastly, we should see higher group productivity in competitor-free environments, and equally low group productivity in competitor-dense environments (P2d; Emery Thompson, 2013; Emery Thompson et al., 2012b).

4.3 METHODS

4.3.1 Study Species

Red-tailed monkeys are small-bodied (males: 3.7, females: 2.8 Kg; Cords et al., 2013), arboreal primates endemic to sub-Saharan tropical forests in East and Central Africa. They inhabit moist lowland, submontane, and montane forests, thriving in both regenerating and primary forest areas, particularly along edges (Cords & Sarmiento, 2013), which are

environments characterized by rapidly changing nutritional landscapes (Houle et al., 2006, 2014). Red-tails have highly diverse and seasonally fluctuating diets (Bryer et al., 2015; Chapman et al., 2002), favoring ripe fruit but also consuming unripe fruit, leaves, flowers, and other plant parts, with increased reliance on insects during lean periods (Bryer, 2020; Chapman et al., 2002; Struhsaker, 2017). Like other frugivorous primates, red-tails typically co-occur with one or more food competitors (Bryer, 2020; Struhsaker, 1978; Waser & Case, 1981), which strongly shapes their access to food (Chapter 2; Steinitz et al., in prep). Studying red-tailed monkeys offers a unique opportunity to gain insight into primate energetics because their broad and flexible diets are representative of those of many other primate species (Chivers, 1980), including endangered and under-studied species.

To draw a comprehensive picture of the physiological costs of competition for red-tailed monkeys, I evaluate a biomarker panel using urine and fecal samples to identify different states of physical condition (Fig. 4.1). I use behavioral observations and urine and fecal samples that I and a team of field assistants collected during a 3-month field season in 2019 from red-tailed monkey groups across four sites: the Rwengobe group (no competitive pressure; Table 4.1), the Mabira group (low competitive pressure), the Ngogo-boundary group (moderate competitive pressure), and one of the Ngogo core groups (strong competitive pressure). I compare these data to existing data from six Ngogo core groups (strong competitive pressure; samples collected by M. Brown in 2012-2019).

4.3.2 Study Sites and Groups

4.3.2.1 *Kibale*

Kibale National Park in western Uganda is a mid-elevation, moist, evergreen rainforest featuring diverse successional stages, including old-growth and secondary forests, swamps,

and grasslands (Chapman et al., 2000; Lwanga et al., 2000; Potts, 2008). The Ngogo Research Station (0.498194° N, 30.424969° E) receives an average annual rainfall of 1427 mm, with considerable variation across seasons (Potts et al., 2020). Kibale National Park is home to twelve non-human primate species (De Jong & Butynski, 2012), of which only four are diurnal, arboreal, and highly frugivirous, and compose a competitive feeding guild: chimpanzees, grey-cheeked mangabeys, blue monkeys, and red-tailed monkeys.

Red-tailed monkeys at the Ngogo Research Station live in stable social groups consisting of multiple adult females, their offspring of varying ages, and one adult male. I studied two groups at Ngogo. In summer 2019, I collected samples from R13 (Ngogo - boundary; Fig. 4.2a) and R1 (Ngogo-core). R13 is located in a boundary zone between two chimpanzee communities and coexists with mangabeys and blue monkeys but experiences very little competition from chimpanzees. Its home range is 0.88 km² and includes 23 individuals (1 M; 9 F; 1 SM; 4 SF; 4 J; 3 I). R1 is one of Brown's long-term study groups and, along with the other habituated long-term study groups (R2-R6), is positioned centrally within the chimpanzee community range. These groups experience competition from mangabeys, blue monkeys, and chimpanzees. In this study, I use the samples and observational data from R1-R6, originally collected by Brown and a team of field assistants as part of a study on intergroup conflicts with conspecifics at Ngogo (Brown, 2013; Jaeggi et al., 2018), and that were later used in a study on red-tailed monkey energetics (Brown et al., 2022; Steinitz et al., *in prep*; Chapter 2 of this dissertation). The six groups vary in size (mean ± SD = 18.17 ± 5.18 adults and subadults per group; juveniles and infants were not included in group size estimates) but have similarly sized and slightly overlapping home ranges (mean 0.37 ± 0.04 km²; Fig. S4.1 of Chapter 2). The home ranges of groups R1, R3, R4, and R6 are positioned almost entirely within the larger mangabey and blue monkey home ranges (Brown, unpub.

Table 4.1. Summary of Red-tailed Monkey Group Characteristics at Various Field Sites in Uganda. The table lists the number of individuals per class (AF = adult female, AM = adult male, SF = subadult female, SM = subadult male, SA = unknown subadult) in the biomarker dataset (N/class), as well as the number of females that transitioned from SF to AF during the study (SF→AF). The competitive guild column indicates the presence (+) of larger-bodied food competitors (BL: blue monkeys; MY: grey-cheeked mangabeys; CH: chimpanzees). The study period details the first and last month of data collected for each group. The groups are listed in decreasing order of competitive pressure.

				Competitive Guild				
Field site	**Group**	**N/class**	**SF→AF**	**BL**	**MY**	**CH**	**Other**	**Study period**
Ngogo	R1	AF: 18, AM: 1, SF: 4, SM: 2, SA: 2	5	+	+	+		1/13-8/19
	R3	AF: 13, AM: 2, SF: 3, SM: 2, SA: 2	3	+	+	+		8/12 - 4/15
	R4	AF: 10, AM: 1, SF: 1, SM: 1, SA: 3	1	+	+	+		12/12 - 7/14
	R6	AF: 19, AM: 3, SF: 3, SM: 3, SA: 11	3	+	+	+		1/12 - 7/17
	R2	AF: 8, AM: 1, SF: 0, SM: 2, SA: 4	2	+ few	+ few	+		8/12 - 2/18
	R5	AF: 15, AM: 2, SF: 0, SM: 1, SA: 5	2	+ few	+ few	+		1/12 - 8/17
	R13	AF: 7, AM: 1, SF: 1, SM: 0, SA: 0	0	+	+	+ few		7/19 only
Mabira	RA2	AF: 8, AM: 1, SF: 1, SM: 1, SA: 0	0		+			6/19 only
Rwengobe	RR	AF: 10, AM: 1, SF: 0, SM: 1, SA: 0	0				+ infreq.	4/19 - 8/19

data). Group R4 lives in a regenerating grassland, which is less biodiverse than the home ranges of the other red-tail groups, and therefore tends to be used less intensively by the other frugivorous species. A significant portion of the home ranges of groups R2 and R5

falls in gaps between the mangabey and blue monkey home ranges, rendering large areas within these red-tail home ranges relatively free of interspecific feeding competition.

4.3.2.2 *Mabira*

Mabira Central Forest Reserve (hereafter, Mabira; Fig. 4.2a), a mid-elevation rainforest, is less than half the size of Kibale National Park but is nonetheless one of Uganda's largest natural and continuous forests, covering approximately 300 km² (Boffa et al., 2008; Jjagwe et al., 2020). The reserve includes old-growth rainforest, secondary forest, and other successional stages, alongside swamps and grasslands. Annual temperatures average 26°C year-round and rainfall ranges from 1250 to 1400 mm. The forest is biodiverse, with hundreds of animal and plant species (Jjagwe et al., 2020). Mangabeys are the only primate food competitors for red-tails (Table 4.1), but other frugivores– large birds, small mammals, and bats– also inhabit the forest. The area has faced significant human encroachment and deforestation, largely due to agricultural expansion and settlement pressures, and plants and animal populations are heavily exploited through illegal resource use. Its botanical diversity includes plant species not present in Kibale National Park (Basiibye, 2020), including the paper mullberry (*Morus papyrifera*), a dominant introduced species that is a major food source for the primates. Tree stems at Mabira are generally smaller in size than those in Kibale National Park, which might correspond with lower fruit production (Minor & Kobe, 2019). An alcove of forest adjacent to Najjembe Village (0.400587° N, 33.014836° E) is home to red-tail group RA2 (Mabira group), consisting of 18 individuals at the time of sampling (1 male; 8 females; 1 subadult male; 2 subadult females; 5 juveniles; 1 infant). Their home range is 0.46 km² with its western boundary abutting the village and on its southern boundary a major highway linking the Ugandan cities of Kampala and Jinja to the border with Kenya.

The group is cohesive and highly social, with individuals spending much of their time in proximity to each other and feeding in the same tree (Steinitz, pers. obs.). I observed a few instances of the adult male crop raiding in the nearby maize field, though this was not a regular occurrence and no other individuals partook in the raiding. I also observed the group spending time by the market along the trucking route that passes through the forest. The adult male and two adult females fed on small amounts of human food scraps (fruit, sugar cane, and some cooked chicken) while most of the individuals adhered to their natural diet throughout the observation period.

4.3.2.3 *Rwengobe*

Forest fragments around Kibale National Park serve as important refuges for biodiversity (Chapman et al., 2003). These fragments can exhibit varying degrees of plant and animal diversity depending on their size, connectivity to the main forest, and level of human disturbance, though they usually do not fully represent the diversity found within the core of the protected area. The Rwengobe fragment (Fig. 4.2a) is located 11.5 km south of Ngogo Research Station, just outside of Kibale National Park (0.394138° N, 30.412109° E) on private property that is surrounded by agricultural fields. Rwengobe is not as diverse as Ngogo, has a lower canopy, as well as a lower density and basal area of most plant species (Basiibye, 2020), all of which are characteristic of a younger, regenerating forest. The fragment is connected to the edge of Kibale National Park by a large papyrus swamp that stretches 2.5 km and is surrounded by open agricultural fields, but this is not a common wildlife corridor as it offers no arboreal substrate for movement or coverage during terrestrial movement. As a result, the Rwengobe red-tail group (1 M; 9 F; 2 SM; 2 SF; 4 J; 4 I) is the only frugivorous primate group in this fragment. Small groups of vervets (*Chlorocebus*

pygerythrus) and mangabeys visit the fragment infrequently, and the red-tails exist without permanent primate competitors. Despite its limited ability to disperse or expand its range, the group is relatively large and does not appear to be food-limited, as it has many independent and dependent juveniles and infants.

4.3.3 Behavioral Observations

Data collection at Ngogo between 2012-2015 is described in detail in Chapter 2 of this dissertation. Data collected for groups R1 and R2 between 2018-2019 follows the same protocols. In short, observers followed two groups simultaneously for 3-6 months, then switched to another pair of groups for several months. Each group was followed for at least two periods, each consisting of multiple consecutive months, during the 3.5 years of observations (Fig. S2.1 in Chapter 2). Observers followed the groups from dawn until dusk every day for one or two weeks (hereafter, "observation periods"), then rested for a week before resuming observations. Each group's observation period consisted of one or two days of conducting a phenology census followed by data collection for the remainder of the observation period. During observation days observers conducted a group scan every 30 minutes. During this scan, they recorded the group's location as the center of mass, and polyspecific associations (details below in section *4.3.4 Determination of Competitive Pressure*), as well as foraging behavior (which was not used in this study; see Chapter 2 - *Behavioral observations*). Individuals were identified using their unique nose shapes, scars and tail kinks, and nipple shape, color, and length in adult females.

4.3.4 Determination of Competitive Pressure

I used two methods for estimating competitive pressure. For groups within a chimpanzee home range, close phenological monitoring of individual food trees that are important for chimpanzees provides an indicator of chimpanzee competition (Chapter 2; Steinitz et al., in prep). Chimpanzees' dynamic fission-fusion behavior makes it difficult to collect comprehensive data on their ranging patterns (Watts, 1998). Despite this, understanding community-wide movements is crucial, since even a single chimpanzee near red-tail home ranges can trigger red-tail monkey behavioral responses (Teelen, 2007; Watts & Mitani, 2002). Chimpanzees consistently travel to and forage in high-yield areas with abundant ripe fruits, which strongly influences their habitat use (Potts et al., 2015, 2016; Wrangham, 1977). Given their predictable reliance on these productive areas, we use the chimpanzee phenology census dataset as a proxy for chimpanzee foraging and ranging patterns (Janmaat et al., 2014; Normand et al., 2009; Wrangham, 1977). The Ngogo Chimpanzee Project monitored fruit production on a set of tree species that are important chimpanzee foods (Watts et al., 2012; Table S2.8 in Chapter 2). Fruit availability is recorded as the percentage of each tree crown bearing ripe fruit (in abundance categories: no fruit, 1-25%, 26-50%, 51-75%, or 76-100%; Chapman et al., 1994). For groups that overlap with mangabeys and blue monkeys, Brown estimated competitive pressure according to the overlap of red-tail home ranges with those of resident blue monkeys and mangabeys (unpub. data). The result is a rough categorization of groups to competitive pressure categories of "high" (R1, R3, R4, R6, R13; Table 4.1), "moderate" (R2, R5), or "low" (Mabira) degrees of competition, or "none" (Rwengobe). Groups R1-R6 exist in the core of the central chimpanzee community, so they experience strong competitive pressure from chimpanzees. Group R13 exists along the boundary between the western and central chimpanzee

communities, an area that chimpanzees rarely travel to (Brown, unpub. census data) because of the risk associated with encountering members of another community (Mitani & Watts, 2001; Muller, 2002). As a result, this red-tail group coexists with mangabeys and blue monkeys, but experiences very little competition from chimpanzees.

4.3.5 Determination of Reproductive Productivity

To test the effect of between-species feeding competition on reproductive investment (P1d and P2d), Brown determined each female's reproductive status per sampling period. 17β-estradiol (estradiol) is a sex steroid which can be assayed from fecal samples (Behringer & Deschner, 2017; Emery Thompson, 2013). This hormone is sensitive to energetic condition and is a mechanism by which reproduction is paused during periods of nutritional shortfall (Ellison, 2003). Estradiol is elevated around ovulation and especially during gestation, and higher levels are associated with a greater likelihood of conception, implantation, and successful live birth (Beehner et al., 2006; Emery Thompson, 2005). Red-tail estradiol levels are 14.2 times higher in pregnant females and 3.8 times higher in cycling (ovulating) females compared to non-cycling females (Brown, unpub. data). To distinguish ovulation from pregnancy, hormonal fluctuations are determined using estradiol values from consecutive daily fecal samples. The status of each female in each sampling period is determined by estradiol levels (cycling and gestational phases of reproduction) and observations of nursing, dependent young (lactational amenorrhea). Each female is assigned a monthly score (0=cycling, no reproductive output; 0.50=non-cycling, amenorrhea– likely recent but not current reproduction; 1=pregnant). Individual reproductive score values are compared across groups to determine if there is variation in reproductive investment as a function of the number of competing species.

4.3.6 Sample Collection

Urine samples were collected non-invasively from the monkeys using clean plastic sheets suspended on long-handled sticks held underneath the monkey as it urinated, or by pipetting droplets from vegetation that was not obviously contaminated by other debris (Knott, 1998). Observers collected samples opportunistically and non-invasively throughout the day with the goal of collecting at least three urine samples and two fecal samples per individual, per observation period. Multiple urine samples per individual, per sampling period are needed to smooth out variation in biomarkers that are susceptible to short-term fluctuations (e.g., post-feeding UCP; Emery Thompson et al., 2009; Girard-Buttoz et al., 2011). Urine and fecal samples were stored on ice packs until 1900 hours, when the team returned to the field station. At camp, urine samples were placed in a solar-powered freezer (-12°C). Fecal samples were later dried at 100°F for 10-12 hours using a Brinsea (Titusville, FL) battery-powered chicken-egg incubator lined with silica beads, and then stored in Whirl-pak bags in a dry, cool storage bin. Samples were transported (urine while still frozen and feces at room temperature) from Uganda to the Hominoid Reproductive Ecology Laboratory at the University of New Mexico and the Biobehavioral Health Laboratory at UCSB, where they were stored in a -80°C freezer until analysis.

4.3.7 Laboratory Analysis - Urine

Laboratory work was carried out at the Hominoid Reproductive Ecology Laboratory at the University of New Mexico and at the Biobehavioral Health Laboratory at UCSB, by both M. Brown and me unless indicated otherwise.

We measured specific gravity, the density of the sample relative to water of urine samples using a digital refractometer (Atago PAL-10S, Omaeda, Japan) to standardize UCP,

creatinine, and ketone values from samples of varying concentrations (Anestis et al., 2009). All UCP values are hereafter reported in units of nanograms of the UCP protein per milliliter (ng/mL; Brown et al., 2022); UCP values spanned five orders of magnitude and were left-truncated (mean = 9.95 ± 23.03 ng/mL), so I $\log_{10}$-transformed the values (Fig. 4.3a); creatinine, which is assayed and measured in mg/mL, is reported as the residuals from a regression of creatinine against specific gravity (CR:SG; Emery Thompson et al., 2012a); and ketones, which are measured in units of mM, are reported in units of mM per milliliter (mM/mL; Naumenko et al., 2019).

4.3.7.1 *Urinary C-peptide*

We assayed UCP for each sample in duplicate using a commercial human C-peptide radioimmunoassay kit (HCP-20K; Millipore Corporation, Billerica, MA), which was cross-validated for use with non-human primate samples (Emery Thompson et al., 2009; Emery Thompson & Knott, 2008; Sherry & Ellison, 2007). Due to highly variable UCP concentrations, many samples were run multiple times at different dilutions (from 1:1 up to 1:50) until the adjusted concentration of UCP fell within the standard binding curve. Assay accuracy, as determined by the recovery of a sample added in duplicate to all points of the standard curve, was (mean ± sd) 101.8 ± 1.5% (N = 6). Parallelism was verified by comparing binding from serial dilution of a sample ($y = -47.4x + 183.8$) to the standard curve ($y = -45.9x + 179.8$, $t = 0.432$, $df = 8$, $p = 0.677$). There is no difference in UCP values from the same group across labs ($t = -1.16$, $df = 83.80$, $p = 0.25$). Intra-assay coefficient of variance (CV) among sample replicates was 6.5%, and inter-assay CV of the manufacturer-provided low and high controls was 8.1% and 7.6%.

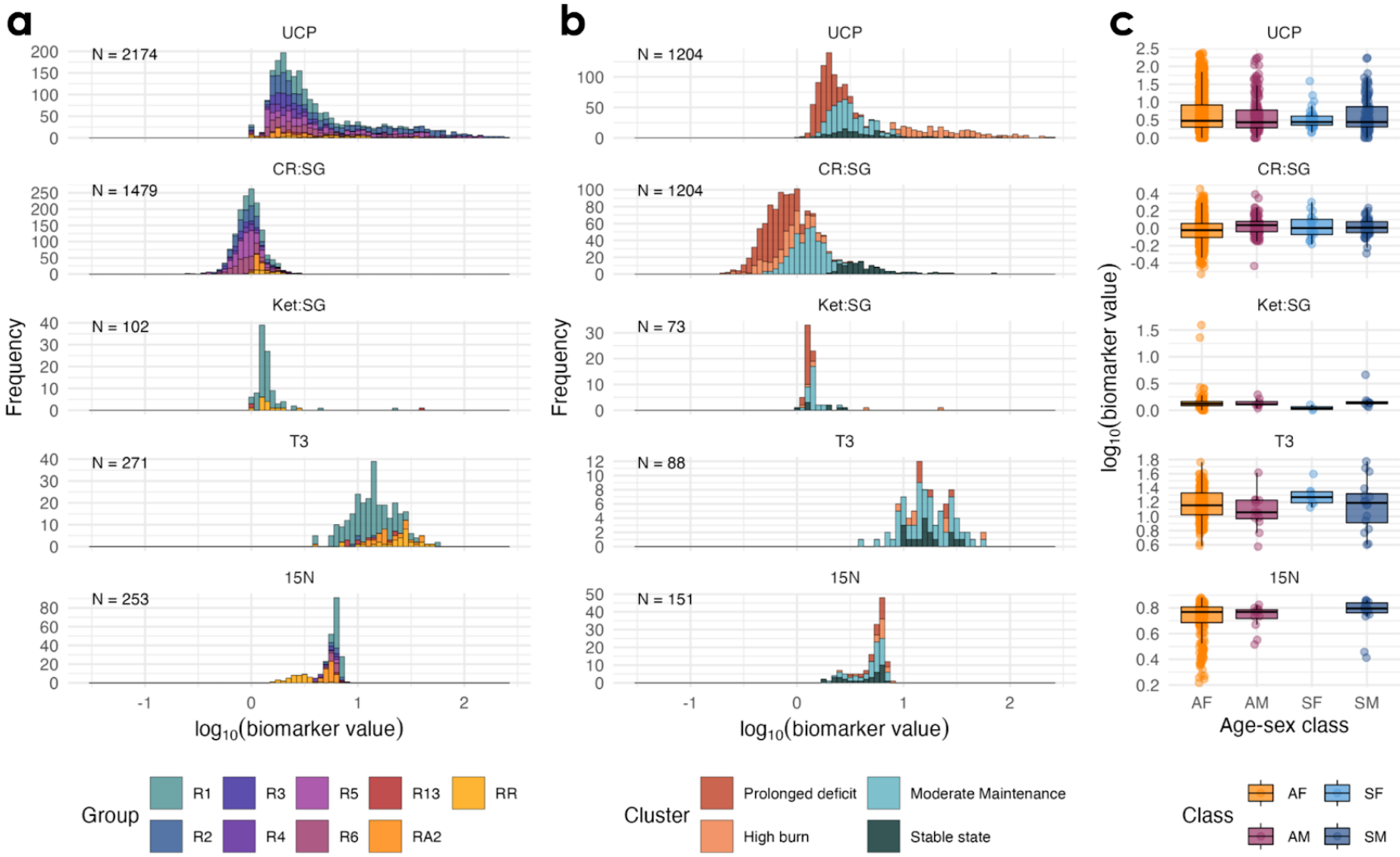
a
UCP
N = 2174
CR:SG
N = 1479
Ket:SG
N = 102
T3
N = 271
15N
N = 253
Frequency
log10(biomarker value)
Group
R1
R2
R3
R4
R5
R6
R13
RA2
RR
b
UCP
N = 1204
CR:SG
N = 1204
Ket:SG
N = 73
T3
N = 88
15N
N = 151
Frequency
log10(biomarker value)
Cluster
Prolonged deficit
High burn
Moderate Maintenance
Stable state
c
UCP
CR:SG
Ket:SG
T3
15N
log10(biomarker value)
AF
AM
SF
SM
Age-sex class
Class

Figure 4.3. Biomarker Data by Group and Age-sex Class. a) The distribution of values in a panel of biomarkers of energetics from nine red-tailed monkey groups across three sites in Uganda. The biomarkers include urinary c-peptide corrected by specific gravity (UCP), the residuals from the relationship between creatinine and specific gravity (CR:SG), ketones corrected by specific gravity (Ket:SG), triiodothyronine (T3), and nitrogen isotope ($\delta^{15}N$). Each panel shows the sample size in the top left corner and a histogram of the frequency distribution of biomarker values in the dataset. Colors represent different red-tail groups surveyed in this study (Ngogo: R1, R2, R3, R4, R5, R6, R13; Mabira: RA2; Rwengobe: RR). **b)** The distribution of biomarker values, with color representing the different metabolic clusters (see Fig. 4.4). UCP and CR:SG were used as the clustering factors, so the number of samples for which clusters were assigned was lower than the total samples in the study (N = 2,174) and determined by data overlap between these two biomarkers (N = 1,204). **c)** Comparison of the biomarker values among different age-sex classes (AF = adult female; AM = adult male; SF = subadult female; SM = subadult male). Boxplots display the median and interquartile range, and jittered points show individual data values, including statistical outliers. All biomarker data are log10-transformed to scale the raw values, some of which span four orders of magnitude and are highly right-skewed.

4.3.7.2 Creatinine

For creatinine, we assayed urine samples in triplicate using the colorimetric Jaffe reaction (Emery Thompson et al., 2012a; Taussky & Kurzmann, 1954). Intra-assay CV among sample replicates was 2.50 ± 1.85%.

4.3.7.3 Ketones

Ketone concentration was measured using a commercially available β-hydroxybutyrate colorimetric assay kit (Cayman Chemicals kit #700190), assayed in duplicate according to the manufacturer's instructions. Ketones are typically analyzed in studies of much larger primates (Knott, 1998; Naumenko et al., 2019), and have never been evaluated in red-tailed monkeys. I validated the Cayman Chemical kit specifically for use with red-tailed monkey urine, evaluating 100 samples. Ketone levels in urine only increase above baseline when the body is actively undergoing ketosis, so I selected samples *a priori* from periods of low fruit availability (calculated for Chapter 2) and matched them with an approximately equal number of samples from periods of moderate to high food abundance for comparison. I validated the kit for use in this species: I verified parallelism by comparing binding from the serial dilution of a sample ($y = 0.0736 + 2.572x$) to the standard curve ($y = -0.0747 + 2.575x$, $t = 0.25$, $df = 26$, $p = 0.81$); mean intra-assay CV = 2.13 ± 0.82% (N = 8).

4.3.7.4 Nitrogen Isotope

For isotope analysis, I pipetted 10μL of each urine sample into a pre-weighed tin capsule, dried at 40°C for 12 h, and then re-weighed the capsules. I subtracted the mass of the empty from the full capsule to produce the net mass of the dry urine sample. Each capsule was then topped off with another 10μL aliquot of the urine sample, and the process was repeated

until the dried mass of the sample was approximately 600-800μg (Vogel et al., 2012). Tin capsules were then pelleted, and shipped for analysis at one of two facilities: isotopic and elemental composition at UC Santa Cruz was determined by Dumas combustion using a Carlo Erba 1108 elemental analyzer (Milan, Italy) coupled to a ThermoElectron Delta+XP isotope ratio mass spectrometer (Bremen, Germany) corrected to International Atomic Energy Agency (IAEA) standards. After this facility went on an indefinite hiatus in 2023, I analyzed the remaining samples (N = 186) at the UC Davis Stable Isotope Facility, using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Analytical precision (standard deviation) of the internationally calibrated in-house standards was 0.12‰ (UC Santa Cruz) and 0.08‰ (UC Davis). The $\delta^{15}N$ values are determined from the relative difference in isotopic ratio between the samples and known standards as represented by the following equation:

$$\delta^{15}N = ((R_{sample}/R_{standard}) - 1) \times 1000$$

where R is the ratio of the heavy to the light isotope ($^{15}N/^{14}N$). Samples are also analyzed for their ^{13}C values (not used in this study), and low C:N ratios in the samples in this study (mean: 3.17 ± 1.63) indicated low lipid content, affirming that lipid extraction was unnecessary (Bearhop et al., 2002). Isotope ratios are reported as parts per mil (‰).

4.3.8 Laboratory Analysis - Feces

Fecal hormone extractions were performed at the UC Santa Barbara Biobehavioral Laboratory, following methods developed for T3 extraction from primate feces (Gesquiere et al., 2014) and field-friendly methods to extract other steroid hormones from feces (Pappano et al., 2010).

4.3.8.1 Triiodothyronine

The T3 extraction process began with agitating 0.1g of sample in 5mL of 70% ethanol for 30 min, then centrifuged. The supernatant was decanted into a tube and set aside. T3 occurs in much lower concentrations in the blood than the other hormones measured here (Levy & Bribiescas, 2023), so the process was then repeated on the same fecal pellet to maximize the extraction per sample. The supernatant from the second agitation of the pellet was then combined with the supernatant from the first round, filtered to remove any remaining fecal residue, and dried down under pressurized air at 37°C. We used the standard 0 from the commercial radioimmunoassay kit (06B254215, MP Biomedicals, Irvine, CA) to reconstitute the supernatant to a 40x concentration of the samples. The same kit was used to assay the samples according to manufacturer instructions, and all samples were measured in duplicate. T3 values are reported in units of ng/dL.

4.3.8.2 Estradiol

To extract estradiol from fecal samples in the field (samples from 2013-2014), each sample was mixed thoroughly using a wood tongue depressor immediately upon collection, and portion was added to 3mL of a methanol:acetone solution (8:2). The mixture was homogenized using a handheld biovortexer and then capped and brought to camp at dusk. The tube was centrifuged for 15 min using a jury-rigged 12V fan, and 2.5mL of the supernatant was pipetted to a new tube. 5.8 mL of distilled water was added to the supernatant and homogenized. The solution was then filtered through a Waters C18 Sep-Pak Plus cartridge pre-conditioned with 2 mL of methanol followed by 5 mL of dH_20. The supernatant-dH_20 mixture was passed through the cartridge, followed by a 0.1% solution of sodium azide to prevent bacterial or mold growth. After the cartridge was dried by storage

with silica gel, the hormones were eluted with 2.5 mL of methanol and stored at -80°C until they were assayed. Samples collected after 2014 were extracted from dry feces: ~0.065g of a sieved dry sample was added to the methanol:acetone solution and placed on an orbital wave roller for 8 hrs to simulate the delay between sample collection and extraction in the field, followed by the same extraction protocol as the wet samples.

We assayed estradiol in duplicate using a commercial radioimmunoassay kit (0713810-CF, MP Biomedicals), which was cross-validated for use with non-human primate samples (Lu et al., 2010; Pappano et al., 2010; Roberts et al., 2012). Brown validated the kit for use in red-tailed monkeys (parallelism: $F_{2,10} = 1004.86$, $p = 0.118$, $N = 13$; accuracy: 125±6.0%; inter-assay CV: low = 5.8%, high = 6.5%; intra-assay CV: 2.9%). Due to highly variable estradiol concentrations, some samples were run multiple times at different dilutions (from 1:1 up to 1:50) until the adjusted concentration fell near 50% binding on the standard curve.

4.3.9 Data Analysis

All data analysis was done in R (v. 2023.12.1.402; R Core Team, 2021; RStudio Team, 2020). Data exploration and visualization used packages from the *tidyverse* (v. 2.0.0, Wickham et al., 2019) unless stated otherwise.

4.3.9.1 *Chimpanzee Competition*

I calculated the chimpanzee competition index per red-tail group home range per observation period for Chapter 2 of this dissertation. I only included data from trees in the chimpanzee phenology census that fell within the home range of each group or within a 100 m buffer zone around the home range because primates perceive predators as a threat at a distance of up to 100m (Ducheminsky et al., 2014; Stankowich & Blumstein, 2005). I

multiplied each ripe fruit score by the tree diameter at breast height (DBH), which correlates with fruit yield (Miller & Dietz, 2004), and summed across species to yield a food abundance index per red-tail home range per calendar month (Chapman et al., 1992; Fig. S2.2 in Chapter 2). The chimpanzee phenology census was not synchronized with the red-tail behavioral observation periods. As a result, a particular chimpanzee census might occur during or between monkey observation periods. We determined the number of days of overlap between a monthly chimpanzee food abundance index value and the red-tail observation periods, and used the degree of overlap to weight the food abundance index to produce a per-observation period competition index ("*CHomp"*).

4.3.9.2 *Metabolic Cluster Analysis*

I designed this study to be carried out with a comprehensive dataset for a cluster analysis, with complete biomarker values for all samples. Due to a series of critical constraints beyond my control in Uganda and the U.S., the study was curtailed before its completion, and both sample collection and analysis were not as extensive as originally planned. For example, only 116 samples from the Mabira group are included in this study, all of which were collected over a single two-week period in 2019. We collected a total of 2,174 urine samples and 1,231 fecal samples from adult and subadult females and males across nine social groups. Biomarker values, with the exception of fasting UCP values, were summarized as the average per individual red-tailed monkey per day to overcome short-term variation and to reduce potential error. The resulting dataset includes the following number of records per monkey-day-hormone: UCP: N = 1,854; creatinine: 1,258; ketones: 100; T3: 124; $\delta^{15}N$: 219. The set of complete observations– i.e., the number of observations for which data for all biomarkers in the panel exists– is extremely limited (N = 9). Observations that

have data for two biomarkers (two-way combinations) are reduced to a limited dataset, and range from N = 1,216 (UCP and CR:SG) to N = 20 (ketones and T3); three-way biomarker combinations are further reduced, and range from N = 154 (UCP, CR:SG, and $\delta^{15}N$) to N = 9 (ketones, $\delta^{15}N$, and T3); and so on. Considering the resulting power limitations, I repurposed the study to test the feasibility and utility of the methods, using a two-step approach: a cluster analysis using a subset of the biomarkers to identify individual physical condition as either good or poor (condition A vs. B-D; Fig. 4.1), followed by a qualitative evaluation of the resulting clusters to identify periods of moderate or severe energy deficit (conditions C and D). The qualitative analysis included the comparison of biomarker values across groups and observation periods to determine which of the red-tail groups are prone to energetic deficits. Results from these preliminary analyses primarily serve to inform future studies.

To confirm the indicators of long-term energy stores as opposed to short-term energy fluctuations (Fig. 4.1), I performed a paired t-test (*PairedData* package; Champely, 2018) comparing the log-transformed mean UCP values between the two sample collection windows: fasting values (morning, from samples collected before 0800 hours) and post-feeding (all other samples). The analysis included only individuals with both morning and afternoon samples collected on the same day (N = 108 individuals), summarized per group to produce a mean value per group per sampling window.

To categorize the physical condition of each individual in each observation period (P1b, P2b), I performed a k-means clustering analysis (De Koster et al., 2019) of biomarkers of good physical condition (CR:SG and UCP), using the *stats* package in R (R Core Team, 2020). I determined the optimal number of clusters (Rousseeuw & Kaufman, 2009; Yuan & Yang, 2019), and assigned a cluster ID to each individual in each observation period. I then

qualitatively assessed the mean values from the other biomarkers (T3, ketones, $\delta^{15}N$) to establish the physiological characteristics of each cluster.

To determine energy mobilization across age-sex classes, I compared the biomarker panel across age-sex classes: adult females (AF), adult males (AM), subadult females (SF), and subadult males (SM). I first conducted a series of ANOVA tests, one per biomarker, followed by post-hoc Welch's t-tests (*stats* package; R Core Team, 2020), which are robust to unequal variances and sample sizes (Derrick et al., 2016), to identify specific pairwise differences for each biomarker. Subadult females were excluded from the $\delta^{15}N$ analysis because no samples from subadult females were analyzed for this biomarker.

4.3.9.3 *Decision Tree*

High values of certain biomarkers are physiologically significant and help identify specific physical conditions (Fig. 4.1). For instance, high CR:SG values correspond with greater relative muscle mass (Emery Thompson et al., 2012a), while elevated ketone levels indicate fat metabolism due to energy deficit (Knott, 1998). To evaluate the biomarker panel, I used a decision tree approach based on predetermined 'high' thresholds for each biomarker: $\log_{10}(UCP) > 1$ ng/mL (as inferred from Sherry & Ellison, 2007; Brown et al., 2022); CR:SG residuals > 0, indicating above-average muscle mass (Emery Thompson et al., 2012a); and ketones > 0.5 mM/mL, indicating ketosis in humans and non-human primates (Laffel, 1999; Naumenko et al., 2019), which corresponds with values of the 3rd quartile of ketones in this study (0.45 mM/mL; min = 0, 1st = 0.22, median = 0.33, max = 38.19). Where no established threshold existed, I used values one standard deviation above the median: T3 > 21.6 ng/dL (min = 2.88; median = 13.64; max = 58.53) and $\delta^{15}N > 5.42$ ‰ (mix = -3.51; median = 4.89; max = 6.59).

Values above the thresholds for biomarkers of energy gain (UCP, CR:SG, T3; Fig. 4.5b) determine *"good"* physical condition (condition A), while values below thresholds indicate *"worse"* conditions (conditions B-D). Despite indicating poor physical condition, high values for biomarkers of energy deficits (ketones, $\delta^{15}N$) were conservatively categorized as "worse" than good physical condition (i.e., instead of a more definitive *"poor"* condition) because no prior data existed for this species, warranting further study to determine the extent of their natural ranges. I first evaluated CR:SG to classify individuals into condition A, reflecting high muscle mass, which can only be the result of prolonged positive energy and protein balance (Emery Thompson et al., 2012a; Vogel et al., 2012). Next, UCP and T3 values were assessed to detect positive energy balance or maintenance (conditions A or B). Ketones were examined to identify negative energy balance (condition C), while $\delta^{15}N$ values were used to mark severe energy deficits (condition D).

4.3.9.4 *Reproductive Productivity*

To evaluate the differences in reproductive productivity among red-tailed monkey groups, I employed a series of Welch's t-tests (*stats* package; R Core Team, 2020) comparing group mean reproductive index per observation period across groups. This test is more robust against the unequal sample sizes and variances in this dataset than an ANOVA (Derrick et al., 2016). The thresholds for significance were adjusted using a Bonferroni correction for the multiple comparisons (Bender & Lange, 2001). To evaluate the differences in $\delta^{15}N$ isotope values across different reproductive statuses (cycling, noncycling, and pregnant) in red-tailed monkeys, a one-way ANOVA was conducted, followed by pairwise comparisons using Welch's t-tests (Derrick et al., 2016).

4.4 RESULTS

Adult females had significantly lower relative muscle mass compared to subadult females (CR:SG: $t(19.7) = -2.94$, $p.adj < 0.05$; Table S4.1). No significant differences were observed for other comparisons across age-sex classes (all $p > 0.05$). Subadult females had lower UCP values compared to adult females ($t(82.5) = 6.65$, $p.adj < 0.001$), and compared to adult males ($t(222) = 3.31$, $p.adj < 0.01$), but other comparisons of UCP did not show significant differences (all $p > 0.06$). All other pairwise comparisons of hormones across classes were non-significant ($p > 0.18$ for T3, $p > 0.10$ for $\delta^{15}N$, $p > 0.14$ for ketones).

UCP from fasting samples was significantly lower than post-feeding samples ($t(5) = 2.59$, $p = 0.049$; mean difference 0.29, 95% CI: 0.00, 0.58). A second paired t-test excluding the one group (R2) with a negative difference revealed an even stronger pattern ($t(4) = 4.32$, $p = 0.01$; mean difference 0.38, CI: 0.14, 0.62). These findings validate this approach for evaluating long-term energy storage compared to short-term energy inputs, and demonstrate a measurable diurnal change in energy mobilization following feeding in red-tailed monkeys.

4.4.1 Metabolic Clustering

The k-means clustering analysis identified four distinct physical condition clusters (Fig. 4.4a; Table 4.2a), each characterized by unique biomarker profiles and energy states. Cluster numbers are arbitrary and do not represent a sequential order. I named and ranked them **in order of decreasing physical condition: Cluster 1**, the *"Stable State"* (N = 119), exhibited high CR:SG, intermediate UCP and T3, and low ketones and $\delta^{15}N$, indicating good physical condition with a balanced energy state. **Cluster 3**, *"Moderate Maintenance"* (N = 394), was

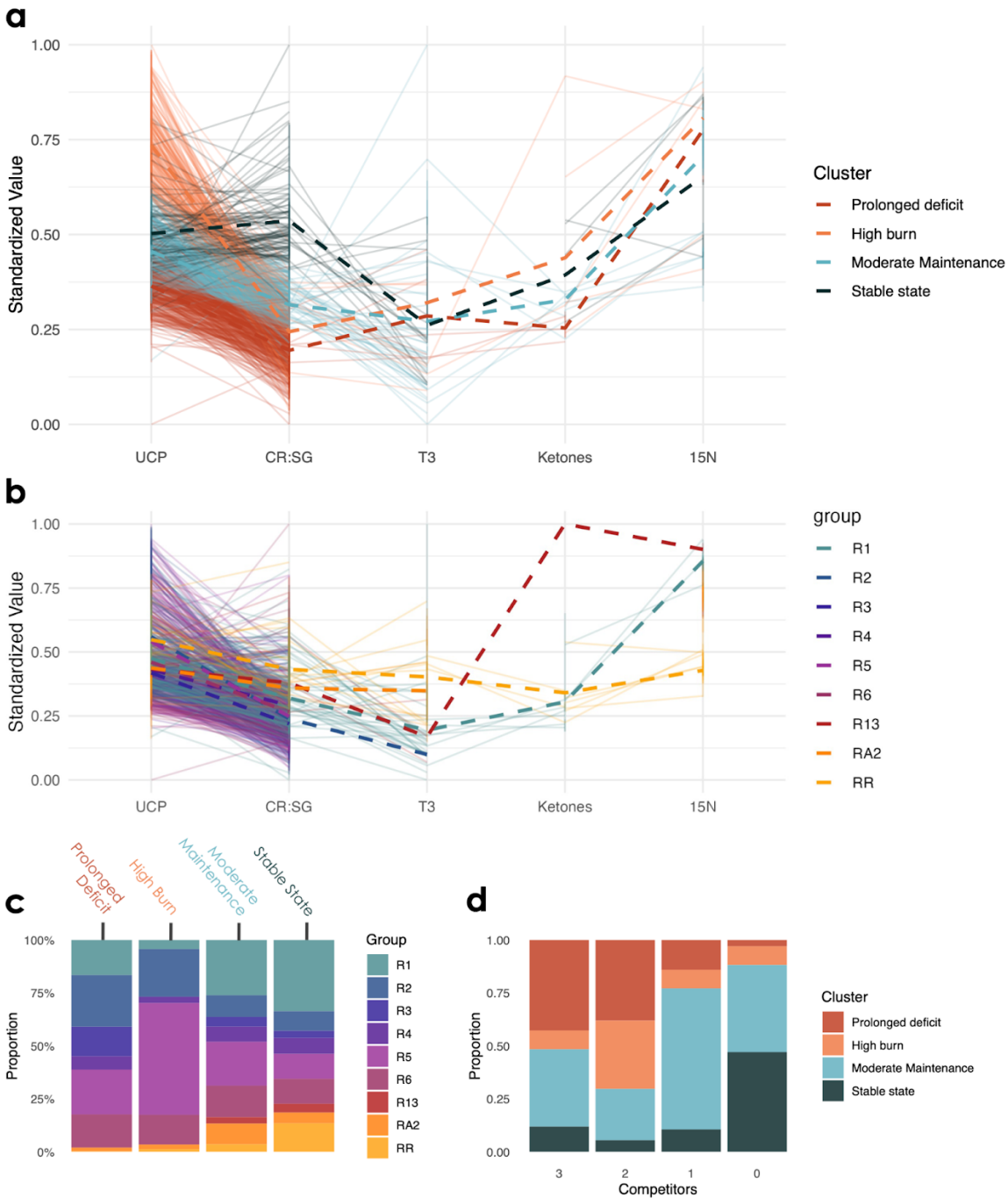

Figure 4.4. Metabolic Clustering by Group and Number of Competitors. Parallel coordinate plots of mean biomarker values per individual per day (scaled between 0 and 1) showing patterns across **(a)** clusters from a k-means clustering analysis of the biomarkers and **(b)** across social groups. Thin colored lines represent an individual sample's biomarker trajectory across the measured variables, and dashed lines indicate global means per cluster (a) and group (b). The emergent patterns highlight inter- and intra-group variability in metabolic profiles. Bar charts show the proportion in each cluster of samples from each

group across metabolic clusters **(c)** and of each cluster across differing numbers of competitors **(d)**. Clusters, in descending order of physical condition, were classified based on their metabolic profiles: Cluster 1= *Stable State;* Cluster 3 = *Moderate Maintenance*; Cluster 2 = *High Burn*; Cluster 4 = *Energy Deficit* (more details in section *4.1 Metabolic Clustering*).

Table 4.2. Biomarker Summary Table. Summary of mean and standard deviation (SD) of measurement of values for biomarkers across A) four clusters identified in a k-means clustering analysis (Fig. 4.4a) and B) across the nine red-tail groups in this study (Fig. 4.4b; Box 1). The biomarkers include urinary c-peptide (UCP), creatinine to specific gravity ratio (CR:SG), ketones, triiodothyronine (T3), and nitrogen isotope (δ15N). Values are reported as mean ± SD for each biomarker within each cluster. (-) symbols indicate that data does not exist for the group. Group colors correspond with the same group colors in other figures; light to dark blue cell colors represent increasing values of biomarkers of good physical condition (darker blue corresponds with higher values and better condition); and light to dark orange represents increasing values of biomarkers of bad physical condition (darker orange corresponds with higher values and worse condition).

A. Biomarker Means Across Metabolic Clusters.

Cluster	**$\log_{10}$(UCP)** ng/mL	**CR:SG** residuals	**T3** ng/dL	**Ketones** mM/mL	**δ^{15}N** ‰
1 Stable State	0.47 ± 0.41	0.66 ± 0.27	17.40 ± 7.79	0.73 ± 0.64	3.65 ± 1.68
3 Moderate Maintenance	1.36 ± 0.38	-0.08 ± 0.20	20.7 ± 17.20	4.43 ± 8.64	4.96 ± 1.28
2 High Burn	0.28 ± 0.26	0.10 ± 0.14	18.00 ± 10.90	0.45 ± 0.26	4.12 ± 1.34
4 Prolonged Deficit	-0.07 ± 0.23	-0.21 ± 0.15	18.80 ± 6.72	0.26 ± 0.07	4.69 ± 0.99

B. Biomarker Means Across Red-tail Groups.

Group	**$\log_{10}$(UCP)** ng/mL	**CR:SG** residuals	**T3** ng/dL	**Ketones** mM/mL	**δ^{15}N** ‰
R1	0.36 ± 0.40	0.11 ± 0.31	13.70 ± 8.97	0.67 ± 2.39	5.36 ± 0.64
R2	0.69 ± 0.71	-0.10 ± 0.26	8.41 ± 0.81	-	5.04 ± 0.64
R3	0.14 ± 0.34	-0.14 ± 0.24	-	-	4.91 ± 0.43
R4	0.19 ± 0.38	0.04 ± 0.28	-	-	3.92 ± 0.93
R5	0.61 ± 0.73	-0.07 ± 0.27	-	-	5.34 ± 0.43
R6	0.30 ± 0.60	-0.02 ± 0.31	-	-	5.03 ± 0.70
R13	0.20 ± 0.22	0.26 ± 0.33	12.70 ± 22.00	12.30 ± 6.39	5.75 ± 0.18
RA2	0.22 ± 0.49	0.21 ± 0.15	22.20 ± 9.00	-	4.37 ± 0.53
RR	0.64 ± 0.42	0.40 ± 0.37	25.30 ± 6.96	0.50 ± 0.42	1.75 ± 1.00

distinguished by intermediate CR:SG and UCP, low T3 and ketones, and intermediate δ^{15}N, reflecting moderate energy management with some stress. **Cluster 2**, *"High Burn"* (N = 235),

was characterized by intermediate CR:SG and T3, high UCP, high ketones, and the highest $\delta^{15}N$ values, showing signs of intense energy expenditure but also energy stress. Finally, **Cluster 4**, *"Prolonged Deficit"* (N = 459), exhibited low CR:SG, low UCP and ketones, intermediate T3, and high $\delta^{15}N$, representing a state of prolonged energy depletion resulting in poor physical condition. The distribution of samples across clusters varied by group and the number of competing species (Fig. 4.4c, d). Groups facing the highest competitive pressure (Ngogo Core groups) had a greater representation in the *High Burn* and *Prolonged Deficit* clusters. In contrast, groups with fewer competitors (Rwengobe and Mabira) and and with reduced competition from chimpanzees (Ngogo boundary) were more frequently represented in the *Stable State* and *Moderate Maintenance* clusters, which are associated with better overall condition and energy balance.

4.4.2 Competition

Despite mixed energy profiles, competition appears to significantly impact the physical condition of red-tailed monkeys. Groups in habitats with more competing species were more frequently in worse physical condition (conditions B-D; Fig. 4.5b) compared to those facing less competition. For instance, RR, which has no competitors, had the lowest $\delta^{15}N$ values across all groups (Fig. S4.3a), indicating they experienced the least severe energetic deficits. Similarly, RA2, which competes only with mangabeys, showed intermediate $\delta^{15}N$ values, comparable to Ngogo Core groups when facing low to moderate competition from chimpanzees (Fig. S4.3b), but the RA2 group had better relative muscle mass.

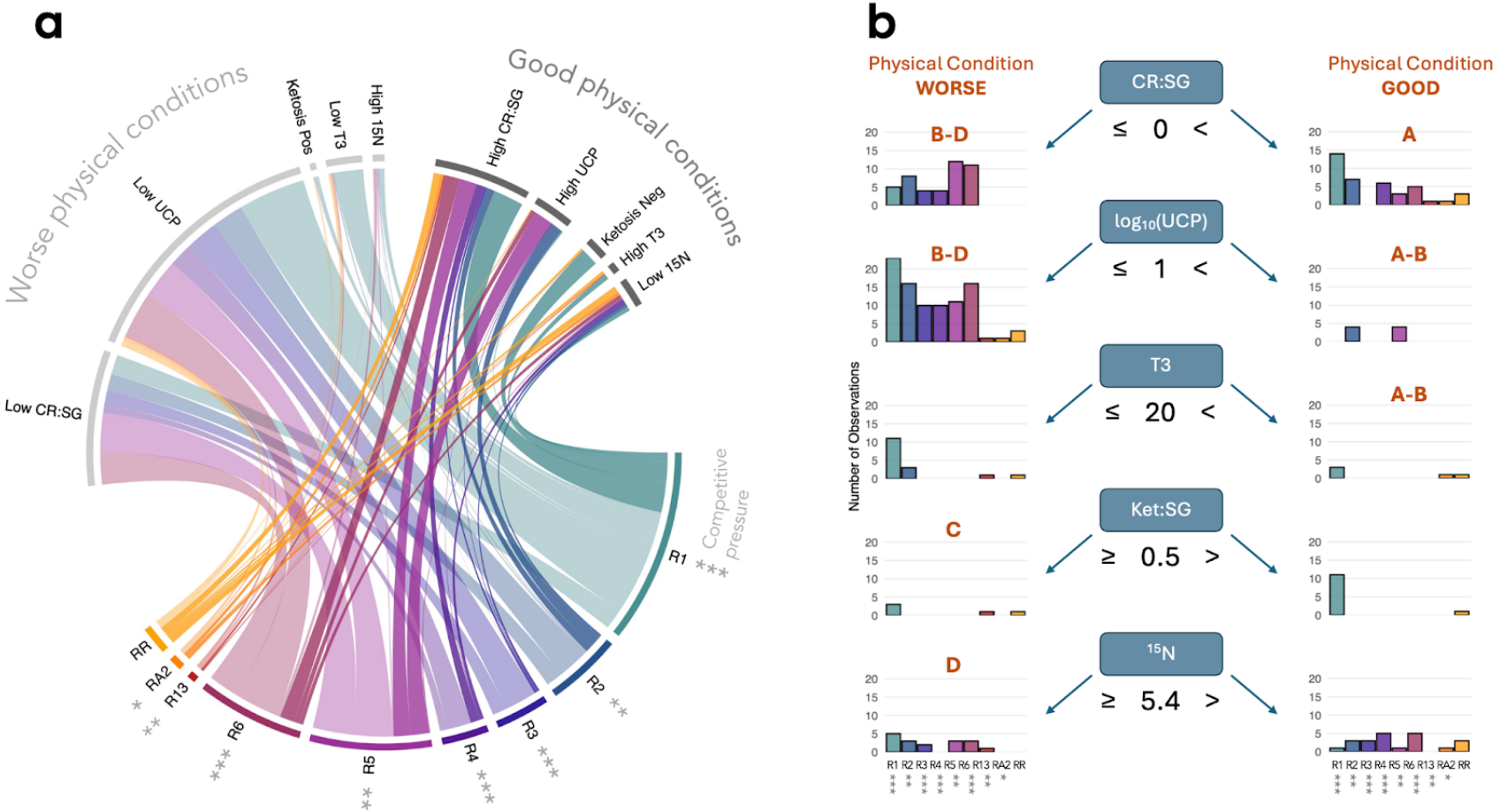
a
Worse physical conditions
Good physical conditions
Ketosis Pos
Low T3
High 15N
High CR:SG
High UCP
Ketosis Neg
High T3
Low 15N
Low UCP
Low CR:SG
Competitive Pressure
R1 ***
R2 **
R3 ***
R4 ***
R5 **
R6 ***
R13 **
RA2 *
RR *
b
Physical Condition WORSE
Physical Condition GOOD
CR:SG
≤ 0 <
log10(UCP)
≤ 1 <
T3
≤ 20 <
Ket:SG
≥ 0.5 >
15N
≥ 5.4 >
B-D
B-D
C
D
A
A-B
A-B
Number of Observations
R1 R2 R3 R4 R5 R6 R13 RA2 RR

Figure 4.5. Physical Condition Categorization and Group Distribution.

a) a chord diagram illustrating the distribution of individual sample biomarker values (Fig. 4.1) associated with "good" (darker links; energy gain; condition A in Fig. 4.1) or "worse" (lighter links; maintenance, or moderate to severe energy deficit; conditions B-D) physical condition categories. The categorization is based on predetermined thresholds (detailed in panel b and in section *4.3.9.3 Decision Tree*), and link transparency represents the relationship between groups and physical conditions, highlighting the proportion of samples from each group associated with each condition. b) bar charts with the number of observation periods in which the group mean was classified as being either good or worse physical condition per the threshold of each biomarker. Orange letters indicate the assigned physical condition category from Fig. 4.1. Asterisks in both panels indicate the relative competitive pressure (none, * = low; ** = med; *** = high; Table 4.1)

Surprisingly, groups with moderate competition (e.g., R13, R5, and R2 at Ngogo) exhibited the highest $\delta^{15}N$ values and below-average relative muscle mass, which is indicative of using muscle mass for energy. The intensity of competition from chimpanzees affected Ngogo Core groups, with elevated $\delta^{15}N$ values occurring more often during periods of high, compared to low, CHomp (Fig. S4.3b). Groups R3, R4, and R6 displayed poor physical condition, characterized by low UCP and CR:SG values, and elevated $\delta^{15}N$ levels. Even groups like R2 and R5, which had higher UCP values, still showed significant nutritional stress, indicating that competition was undermining their ability to maintain muscle mass. The Ngogo Boundary group, R13, presented mixed indicators of physical condition but also exhibited signs of severe energy deficit. In contrast, the Rwengobe group (RR), free from competition, exhibited the best overall condition, with high UCP, high T3, and low $\delta^{15}N$, highlighting the benefits of competitive release on energy gain.

Generally, poor physical condition seems to broadly correspond with the presence of competitors. In biomarkers that indicate prolonged energy gain and prolonged deficit (CR:SG– relative muscle mass; $\delta^{15}N$– muscle catabolism, respectively), groups with fewer competitors (RA2 and RR) spent a higher proportion of their time in "good" physical condition compared to those with more competitors, who spent more time in "worse" physical condition (Fig. 4.6). However, the pattern is non-linear with increasing competitive pressure.

4.4.3 Reproductive Productivity

We found several significant differences in reproductive productivity across red-tail groups. The mean group reproductive index for group R1 was significantly higher than that of group R2 ($t(36.46) = 2.88$, $p < 0.01$), and R2 was significantly lower than R3, R4, and R5

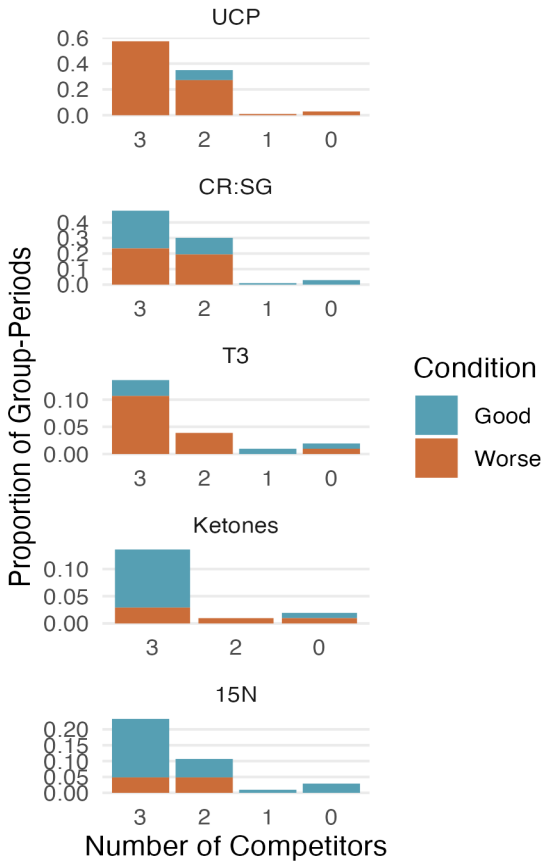

Figure 4.6. Physical Condition Across the Competition Gradient. The proportion of biomarker values per group per observation period categorized as either "good" or "worse" physical condition category (condition A vs. B-D from Fig. 4.1) across a gradient of competing species. The category is defined by biological thresholds for each biomarker (Fig. 4.5; see section *4.3.9.3 Decision Tree*). The x-axis indicates the number of competitors (see Table 4.1), and the y-axis shows the proportion of group-periods categorized in each condition.

(R2 vs. R3: t(11.13) = -2.63, p = 0.02; R2 vs. R4: t(24.60) = -2.40, p = 0.02; R2 vs. R5: t(9.22) = -3.06, p = 0.01). Group R5 had a higher reproductive index than group R6 (t(9.52) = 2.37, p = 0.04). No other comparisons among the groups were significant (p > 0.06), suggesting that, aside from these highlighted differences, the groups exhibited relatively similar mean reproductive productivity. No differences were found between groups with differing competitive pressures (Fig. S4.4).

$\delta^{15}N$ values varied across reproductive statuses (cycling, non-cycling, and pregnant; Fig. S4.5a). Pairwise comparisons showed that pregnant females had significantly higher $\delta^{15}N$ values compared to both cycling ($t = -3.25$, $df = 19.6$, $p < 0.01$) and non-cycling females ($t = -4.59$, $df = 17.6$, $p < 0.001$). No significant difference was found between cycling and non-cycling females ($t = 0.36$, $df = 29.5$, $p = 0.72$). Reproductive status across the four clusters varied slightly in terms of their distribution (Fig. S4.5b). The *Stable State* cluster exhibited a mean status value of 0.50 ± 0.26 ($N = 71$). *High Burn* had the highest mean status value at 0.57 ± 0.32 ($N = 75$). The *Moderate Maintenance* cluster showed a mean status value of 0.50 ± 0.24 ($N = 200$), and the *Prolonged Deficit* cluster had the lowest value (0.42 ± 0.26; $N = 274$). Pregnant females had the highest proportion of females categorized as *High Burn* and the lowest proportion of females in *Prolonged Deficit* (Fig. S4.5c).

4.5 DISCUSSION

The results of this study reveal a complex relationship between competition, energy balance, and reproductive success in the small-bodied red-tailed monkeys. Contrary to patterns observed in other herbivore communities, competition influenced energy balance non-cumulatively.

4.5.1 Additive vs. Universal Effects of Competition

4.5.1.1 *Hypothesis 1 - Additive Effects*

Our findings do not support the *Additive Effects Hypothesis* (H1), which posits that red-tailed monkeys experience increasing energetic suppression as the number of larger-bodied competing species increases. While the Rwengobe group (RR), with no competitors, exhibited the highest UCP levels and better energy balance (P1a), groups in the Ngogo core

and boundary areas displayed inconsistent energy conditions despite varying degrees of competition. This pattern indicates that competition does influence energy balance, but not in a straightforward, cumulative manner as proposed (P1b).

The presence of chimpanzees in the Ngogo core area is associated with energy deficits in some groups (P1c), but similar deficits in groups with less competition from chimpanzees, like R13, imply that chimpanzees are not the sole drivers of these energy imbalances. Additionally, the expected negative relationship between reproductive productivity and the number of competitors was not consistently observed (P1d). For instance, despite experiencing some competitive release from mangabeys and blue monkeys, groups R2 and R5 showed opposite reproductive outcomes. This suggests that the relationship between competition, energy balance, and reproductive success is more complex and may involve other factors beyond the number of competitors, including the impact of specific competitors like mangabeys, and the quality of the habitat. Despite actively pursuing associations with them, red-tail energy balance decreases with increasing associations with mangabeys (Table S2.4 of Chapter 2), suggesting a more complicated tradeoff between the costs of competition and the benefits of protection from predators.

4.5.1.2 *Hypothesis 2 - Universal Effects*

The hypothesis that larger-bodied competitors have a universal suppressive effect on smaller consumers is supported by several key findings. Groups with any competitors, regardless of the number, generally experience energy deficits, which aligns with the prediction that competition from even a single larger-bodied species suppresses energy balance (P2a). The RR group, which is competitor-free, shows energy gain (category A), while all other groups with competitors fall into categories B through D, confirming that the

presence of competitors significantly reduces the likelihood of maintaining an energy surplus (P2b). I do not have enough information to deduce whether the reversal of the food-energy relationship in competitor-dense environments is universal (P2c), and future work will need more comparable measures of food availability across field sites. Even though all groups with competitors experience some energy deficits, regardless of the number of competitors, longer-term data on the groups experiencing less competition (RA2, RR) are necessary in order to establish whether these patterns are consistent over long periods of time and with fluctuating food abundance.

Lastly, the absence of a discernable pattern in reproductive productivity, and the unexplained high reproductive index in an energetically stressed cluster (*High Burn*), contradicts my prediction that competitor-dense environments result in lower reproductive productivity (P2d). More comprehensive data, especially for the less-studied groups, would elucidate longer-term patterns. Overall, the results described here provide support for the *Universal Effects Hypothesis* (H2), indicating that the presence of even a single larger-bodied competitor leads to energy deficits in red-tailed monkeys, regardless of the number of competitors. The physical condition of the groups appears to be universally suppressed by competition, rather than being an additive function of the number of competing species.

Despite empirical support for the *Additive Effect Hypothesis* across ecosystems and taxa (Nascimento et al., 2011, Prins & Olff, 1998), we found no evidence that this reflects the ecological reality of the red-tailed monkeys in this study. Furthermore, while it is highly plausible for a large and dominant competitor to exclude a subordinate species regardless of the number of other competitors in the habitat–i.e., *Universal Effects Hypothesis*–there is a gap in the literature in terms of demonstrating this interaction and documenting its energetic or reproductive outcomes. One study of salmon-stream competitive guilds in North America

describes subordinate black bears that consistently avoid food sources when dominant and highly aggressive brown bears are present, regardless of the presence of other competitors, like wolves (Levi et al., 2020). This behavior might imply a *universal* suppression of black bears. However, the degree of suppression is only roughly estimated—categorized simply as avoidance or approach to food sources—and neither the behavior nor its outcomes are fully quantified. As a result, it remains unclear whether this interference competition leads to similar physiological outcomes in the subordinate species across different community compositions.

Predation pressure, much like competition from larger-bodied species, suppresses energy balance across different species (McGrosky & Pontzer, 2023). In the presence of predators, smaller animals tend to adopt energy conservation strategies, leading to reduced energy stores and lower overall energy expenditure, regardless of the specific predator or the number of predators involved. Predation influences total energy expenditure by causing individuals to flee, hide, or reduce foraging, which can lead to lower energy intake and increased physiological stress (McNab, 1986; Pettett et al., 2017). European hedgehogs, for example, exhibit lower energy expenditure in the presence of predators but higher energy expenditure when food is scarce, suggesting that energy conservation strategies are favored under predation pressure (Pettett et al., 2017). Across taxa, increased predation pressure is associated with reduced internal energy stores and smaller body sizes, which may enhance escape performance and reduce exposure to predators (Macleod et al., 2005; Speakman, 2018; Zimmer et al., 2011). Though we originally assumed that chimpanzees exert such intense competitive pressure on red-tails that no amount of other competitors might impact red-tails in the same way, it is clear that release from the competition of mangabeys and blue

monkeys indeed results in better outcomes, suggesting that competitive pressure by different species might impose similar constraints.

A multi-species lens might explain the higher-than expected energy balance observed in some of the groups. Groups with high energy balance but relatively poor physical condition, like those in the *High Burn* cluster, might prioritize rapid mobilization of energy toward survival and reproduction over investment in longer-term fat stores (i.e., faster life histories; Harvey & Clutton-Brock, 1985) in competitor-dense environments. This cluster is characterized by low fat stores and high reproduction scores, and includes mostly Ngogo Core groups, which experience competition of varying degrees from chimpanzees, mangabeys, and blue monkeys. The extreme effect that chimpanzees have on red-tails might be in part because of their dual roles as competitors and predators. However, mangabeys and blue monkeys, which are both protective and competitive for red-tails, might have an equally detrimental effect on red-tail energy gain. Despite the differences in the dynamics of these interspecific relationships, the net energetic costs and benefits might be equal. Consequently, red-tails might tolerate the competitive pressure they experience while associating with mangabeys because it reduces their extrinsic mortality, a short-term price that seems worth paying for increasing survival and life-long fitness.

Interpreting the differences among the red-tailed monkey groups is inherently limited by the small number of replicates per competitive guild in this study (e.g., samples from only one group with no competitors, RR, over a span of only two weeks). This constraint makes it challenging to draw broad conclusions or definitively assign cause and effect based on such a small sample size. While using individuals as a random effect can improve statistical power, the limited replication of groups leaves open the possibility that the observed differences are driven by factors beyond the hypotheses tested here. A larger sample of

territories would be necessary to generate stronger statistical support. Nevertheless, the observed patterns align with the predictions, suggesting that the *Universal Effects Hypothesis* remains a plausible explanation.

Some questions still remain– do other competitors have the same protective/competitive dynamics that mangabeys have with red-tails? Do blue monkeys assume the top-competitor role in the absence of mangabeys and chimpanzees? Lastly, do chimpanzees from other communities, which hunt monkeys at far lower rates than seen at Ngogo, have the same strong effect on red-tails?

To elucidate the intricacies of these relationships, a potential approach might be to include field sites with different combinations of these and other competitors. Semuliki National Park - on the border between Uganda and the Democratic Republic of Congo - has a larger frugivorous guild that includes mangabeys, blue monkeys, and chimpanzees, as well as other guenons that are closely related to red-tails and blue monkeys (De Jong & Butynski, 2012). Conversely, other forest fragments near Kibale National Park hold different frugivore guild compositions. More diverse frugivorous primates guilds might help identify the effects of competition on other small-bodied primates, and comparing them to red-tails can strengthen the observations made here. In addition, sites where red-tails coexist with a single, non-mangabey, competing species can help determine the effect that specific competitors have on red-tails. The benefits that red-tails incur from their associations with mangabeys must be higher than the cost of competition, but this relationship might change in the absence of other competitors or with reduced predation pressure. Lastly, another field site in Kibale National Park might hold answers about the effects of chimpanzees as predators of red-tails; Kanyawara, a site approximately 11km Northeast of Ngogo, is home

to a smaller community of chimpanzees with lower rates of hunting (Mitani & Watts, 2001; Watts & Mitani, 2002).

4.5.2 The Utility of a Cluster Analysis

The k-means clustering analysis proved to be a valuable tool in categorizing individuals based on their biomarker profiles, offering insights into the physical condition and energy gain of red-tailed monkeys across different environmental and social contexts. The distribution of groups across clusters aligned with our general prediction that groups with more competitors will find themselves in poorer physical condition more frequently than groups with fewer competitors. However, one of the main challenges we encountered was that assigning specific physical condition categories to each cluster was not always straightforward. In descending order of physical condition (*Stable State*; *Moderate Maintenance*; *High Burn*; *Prolonged Deficit*), they only loosely correspond to the physical condition categories (A-D in Fig. 4.1). The clusters often exhibited characteristics that spanned multiple condition categories. For example, the *High Burn* cluster is characterized by high energy balance, a measure that is often associated with good physical condition (Bergstrom et al., 2020; Deschner et al., 2008), higher body mass (French et al., 1992; Yoshida et al., 2006), and reproductive expenditure (Emery Thompson, 2013; Rangel Negrín et al., 2021), which reflect long-term trends in sufficient energy gain. However, this cluster also exhibits low relative muscle mass and signs of ketosis and potential starvation, which are the result of significant energy stress and deficits. This discrepancy illustrates the need to view physical condition as a multi-faceted spectrum rather than discrete states of "good" or "bad" physical conditions.

The life history traits of primates, such as the timing and energy investment in a reproductive bout, are determined by environmental limitations in resources (Harvey & Clutton-Brock, 1985). Metabolic profiles are shaped by constant and highly dynamic tradeoffs in energy mobilization across various physiological demands, such as maintenance, immune function, reproduction, growth, and even social interactions (Pontzer, 2015). Energy expenditure is dominated by *basal metabolic rate* and leaves a narrow margin for energy allocation, so any surplus energy must be allocated carefully in response to continuously monitored environmental pressures. The complexity of these relationships is further apparent with the integration of reproductive productivity data in our analysis. Clusters with better energy profiles did not show higher reproductive output, and the *High Burn* cluster had high reproductive productivity despite clear energy deficits. This might reflect an adaptive strategy where energy is prioritized for reproduction at the expense of other physiological functions.

Energy allocation is a dynamic process influenced by extrinsic environmental pressures as well as intrinsic physiological and reproductive demands. During periods of high reproductive output, such as gestation and early lactation, energy demands spike, often resulting in negative energy balance (Butler & Smith, 1989; Emery Thompson et al., 2012b; Rangel Negrín et al., 2021). Fat reserves buffer periods of energy shortfall, allowing individuals to survive and reproduce despite temporary deficits (Brockman & Van Schaik, 2005; Emery Thompson, 2013). Many species conceive during low food periods but wean offspring when food is abundant. As long as the mother stores enough fat beforehand, she can tolerate negative energy balance during pregnancy and lactation. Red-tailed monkeys reproduce year-round but most births occur from January-March (Cords, 1984), coinciding with the dry season (Fig. S2.1 in Chapter 2). The latter part of their six-month pregnancy

overlaps with the long wet season, between September and November, when EVI is the highest (Fig. S3.2 in Chapter 3). This period aligns with the highest UCP values throughout the year (Fig. S2.1 in Chapter 2). These observations suggest that red-tails align more with the capital breeding end of the life history spectrum (Drent & Daan, 1980; Emery Thompson, 2013) and rely on accumulating sufficient energy reserves during the wet season to support the energetically demanding period of lactation during the dry season. This may explain why the *High Burn* cluster shows high reproductive productivity despite clear energy deficits, as fat reserves could compensate for the immediate energy shortfall. The prioritization of reproductive energy needs can lead to fluctuations in physical condition, where individuals might undergo short-term energy deficits in favor of ensuring reproductive success. For example, energy demands for access to mates or pregnancy might reduce the energy available for immune function or growth (females: Archie et al., 2014; males: Muehlenbein & Watts, 2010; Prall & Muehlenbein, 2014), leading to fluctuations in physical condition that do not align neatly with static energy categories. High energy throughput, while costly, is associated with increased reproductive output in environments where food resources are abundant (Pontzer et al., 2010). In the case of the *High Burn* cluster, their ability to sustain high reproductive productivity despite physiological stress suggests a strategy where energy is heavily allocated to reproduction, possibly as a response to environmental conditions that favor immediate reproductive success over long-term physical maintenance.

Some limitations have also become apparent through this analysis. The non-linear nature of these findings across the competitive gradient underscores the need for further exploration of this method, and the importance of incorporating additional behavioral and ecological data alongside clustering analyses to better capture the tradeoffs between physical condition and reproductive strategies. Additional limitations of this clustering method

include its sensitivity to the distribution of data (Khandare & Alvi, 2016), especially given the low sampling from some groups and missing data for certain biomarkers in my dataset. This may result in clusters that do not accurately reflect the true variation in physical condition across subjects. Furthermore, k-means assumes clusters are of similar size, which was not the case in my dataset, potentially skewing the results.

Lastly, clustering based on only two biomarkers oversimplifies the complexity of physical condition, possibly masking important variations that would be evident with more biomarkers. This reduction in dimensionality can lead to less distinct clusters and a limited ability to represent meaningful physiological states, ultimately affecting the accuracy of the interpretations. A cluster analysis of the physical condition of dairy cows used a set of four metabolic biomarkers to detect how individuals cope with the challenge of lactation (De Koster et al., 2019). With a smaller though more complete dataset, their highest energy profile exhibited similar characteristics to my *Stable State* cluster: increased tissue growth and circulating glucose, and decreased ketones and fatty acids (a biomarker of lyposis). Using more comprehensive data, the metabolic biomarker clustering was successfully used to predict productivity; clustering corresponded with energy balance, weight gain, and milk production, which reflect good overall physical condition. The pattern of energy deficits among groups with several competitors compared to groups with less or no competitors demonstrate the feasibility of this approach, and a larger dataset has a potential to produce a strong modeling method for metabolic profiling of individuals and groups over time.

4.6 Conclusion

This study explores the impact of interspecific competition on the energetic condition and reproductive success of red-tailed monkeys, focusing on how these small-bodied

primates navigate the challenges posed by larger competitors within their shared habitats. The research is set against the backdrop of understanding the broader ecological and evolutionary pressures that shape primate communities, particularly the effects of competition on energy allocation and reproductive strategies. Given the increasing anthropogenic pressures on these ecosystems, understanding the intricate dynamics of interspecific competition is crucial for both theoretical insights into primate ecology and practical conservation efforts (Chapman et al., 2006).

To investigate these dynamics, I employed a novel methodological approach, combining a comprehensive biomarker panel with cluster analysis to assess the metabolic profiles of different groups of red-tailed monkeys. This approach allowed for a more detailed understanding of how various groups, each facing different numbers of competitors, manage their energy budgets. My findings reveal distinct metabolic profiles associated with varying degrees of competition. Groups with more competitors, despite living in more intact habitats, generally exhibited signs of energy deficits, such as positive ketosis and potential protein catabolism, while those with fewer competitors, in smaller or slightly degraded habitats, maintained better physical conditions, as indicated by higher energy balance levels and high relative muscle mass. These patterns suggest that the presence of even a single larger competitor can significantly impact the energy balance of red-tailed monkeys, supporting the hypothesis of universal suppressive effects of competition. Notably, this is the first study to report ketone and nitrogen isotope values for this species, providing critical baseline data for future research.

The use of a biomarker panel addresses a full spectrum of physical conditions and distinguishes different stages of energetic stress, which pose varying constraints on life history and fitness (Emery Thompson, 2017). The preliminary nature of the data means that

while the trends are suggestive, they are not yet conclusive, highlighting the need for further, more comprehensive studies to confirm these findings. Despite this, the results offer valuable insights into primate ecology and social behavior. This new approach to studying interspecific competition is relevant not just to current competitors, but to past ones as well. Understanding how community composition shapes the energetic costs of competition– i.e., whether the physiological costs are amplified by multiple competitors or are constant across a gradient of competitive pressures– can strengthen reconstructions of community dynamics among sympatric hominin species (Bobe & Behrensmeyer, 2004; Froehle & Churchill, 2009). Answering these questions can also aid in future projections of how best to promote coexistence of endangered species, especially in fragmented and degraded habitats where interspecific competition may be intensified. (McLennan et al., 2017).

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V. Under Pressure: Physiology, Energy Mobilization, and Evolution in Competitive Environments

5.1 Introduction

Energy serves as the essential currency connecting all living organisms, driving the complex web of life by moving from the environment to individuals and sustaining biological processes at every level (Odum, 1968). The amount and distribution of energy in a habitat shape ecological communities (Gallagher et al., 2017), with competition playing a central role in structuring food webs within them (Tilman, 1982, 2007). Species with similar needs compete for limited resources like food, water, and space, influencing population growth, distribution, and evolutionary adaptations (Hutchinson, 1959; MacArthur & Levins, 1967; Schluter, 2000). This competition can drive coexistence through resource partitioning or lead to exclusion, as species must adapt to survive (Connell, 1983). These dynamics are particularly relevant in primate communities, which are characterized by overlapping ecological niches and complex feeding guilds, yet they remain understudied (Schreier et al., 2009). Primates tend to occur among one or more food competitors, so revealing the physiological strategies that they use when faced with disruptive food shortages can elucidate the mechanisms that allow species to coexist (Kamilar & Ledogar, 2011; van Holstein et al., 2024).

The strongest factors that shape a species' ecological role are the characteristics of its environment, the competition it experiences from competitors, and its intrinsic traits (van Holstein et al., 2024). This dissertation introduces novel approaches within the field of primate feeding ecology, designed to address these three components shaping ecological niches in the context of interspecific competition among primates in a tropical rainforest environment. The costs of competition are notoriously challenging to measure,

and as a result, little information exists on its physiological outcomes. To develop a stronger understanding of these relationships, my first objective was to **quantify the effects of feeding competition from a large-bodied competitor on a small-bodied primate by using a physiological biomarker of energy gain,** as a measure of food intake in response to food availability and competitive pressure (Chapter 2). In doing so, I discovered that the traditional methods of measuring food availability, a significant component of most studies of primate feeding ecology, do not accurately represent what is actually accessible to species that are low-ranked in the competitive hierarchy. Therefore, my next goal was to **test the effectiveness of a remote-sensed vegetation index, an alternative, broader, and more objective measure of habitat quality, as a predictor of primate foraging behavior** (Chapter 3). Finally, to gain a more comprehensive perspective on the energetic costs of competition, I **assessed whether strong competition can lead to prolonged deficits that affect physical condition and reproduction** by evaluating a panel of metabolic biomarkers showcasing different aspects of energy mobilization (Chapter 4).

Kibale National Park in Uganda provides a compelling model for studying the costs of interspecific competition, with its diverse community of frugivorous primates that share overlapping diets based heavily on fruit. The feeding guild includes chimpanzees (*Pan troglodytes*), grey-cheeked mangabeys (*Lophocebus albigena*), blue monkeys (*Cercopithecus mitits*), and red-tailed monkeys (*C. ascanius*), structured by a size-based hierarchy that dictates access to preferred resources (Bryer et al., 2013; Houle et al., 2010; Struhsaker, 1978). Chimpanzees, at the top of the hierarchy, are both competitors and predators of red-tailed monkeys. They dominate fruit resources due to their large size and potentially aggressive behavior, monopolizing high-value areas and forcing smaller species to alter their foraging strategies to avoid direct competition and predation. Grey-cheeked mangabeys, although significant

competitors for fruit, maintain a complex relationship with red-tails. Red-tails benefit from reduced predation risk through polyspecific associations, making mangabeys both competitors and occasional allies (Bryer et al., 2013; Struhsaker, 1978). Blue monkeys, occupying an intermediate position, exert a more neutral competitive influence but still impact red-tails' foraging behavior in areas with scarce resources (Houle et al., 2006).

Red-tailed monkeys, at the bottom of the hierarchy, have a diverse diet but are heavily constrained by larger competitors, particularly chimpanzees. Their position at the bottom of the competitive hierarchy and the need to avoid predation make them especially vulnerable to the energetic costs of competition. Despite the general link between food abundance and reproductive success in other species (Boutin, 1990; Doonan & Slade, 1995; Lack, 1947; O'donoghue & Krebs, 1992; Wauters & Lens, 1995), red-tailed monkeys do not exhibit increased reproduction with greater food availability (Rode et al., 2006). This disconnect demonstrates that food availability on its own does not determine energetic outcomes for these primates. I found that strong competition from larger guild members limits their ability to fully benefit from available resources, complicating the relationship between food abundance and fitness outcomes.

Red-tailed monkeys navigate a competitive landscape shaped by intraspecific, intergroup, and interspecific competition, each influencing their foraging behavior, physical condition, and overall fitness. Within social groups, red-tails experience intraspecific competition for food, with group size influenced by resource availability (Bryer et al., 2013; Chapman & Chapman, 2000). Though typically less aggressive than other cercopithecines, red-tails still engage in both contest and scramble competition for limited resources (Chapman & Chapman, 2000). Intergroup competition further affects access to foraging areas, as groups defend key feeding sites, particularly when high-value resources like ripe fruits are available

(Isbell, 1991). These dynamics influence group movements and social interactions as red-tails seek to secure food while avoiding costly confrontations (M. Brown et al., 2022; Struhsaker, 1978).

Interspecific competition, particularly from larger frugivores like chimpanzees, exerts strong pressure on red-tails. These dominant species monopolize high-quality resources, forcing red-tails to adjust their foraging strategies and rely on less nutritious foods (Bryer et al., 2013; Houle et al., 2010). The size-based dominance hierarchy leaves red-tails consistently outcompeted, leading to prolonged energy deficits and increased foraging effort (Ganzhorn, 1999). However, during food scarcity, intraspecific competition becomes significant due to overlapping dietary needs and behaviors within their groups. While red-tails can mitigate interspecific competition by adjusting their niche, such flexibility is limited within their social groups, intensifying competition during resource shortages (Lambert & Rothman, 2015; van Holstein et al., 2024). Ultimately, interspecific competition should exert a pervasive, long-term impact on red-tails' ability to access high-quality resources, while intraspecific competition might intensify under direct conflicts for shared, limited food sources, particularly during scarcity.

The Kibale primate guild is an ideal model for studying the energetic costs of interspecific competition due to the clear size-based hierarchy, the overlapping diets, and the dynamic interactions between species. The presence of predators like chimpanzees within the guild adds another layer of complexity, as red-tails must balance the dual threats of competition and predation. The well-known natural history of the forest provides a rich context for exploring how interspecific competition shapes energy allocation, physical condition, and reproductive success. Distinct and well-known boundaries between the social groups of the three larger competitors offer a spatially defined range of competitive

pressures. This novel attempt to quantify competitive pressure in a biodiverse tropical rainforest not only enhances our understanding of primate ecology but also provides insights into the broader ecological processes that govern species interactions in complex environments. This knowledge is crucial for informing conservation strategies, particularly as these species face increasing pressures from habitat loss and climate change (Estrada et al., 2017).

5.2 Main Findings

The findings from this dissertation provide valuable insights into the energetic and ecological dynamics of small-bodied primates, particularly red-tailed monkeys. Each chapter contributes to our understanding of how these primates navigate the challenges of food availability and competition, ultimately offering a more comprehensive view of the interplay between these factors and energy balance.

Chapter 2 demonstrates that red-tailed monkeys do not experience a straightforward, positive relationship between food availability and energy balance. Instead, the interaction between food availability and competition from larger frugivores significantly modifies these outcomes. For example, red-tails benefit from increased fruit availability only when chimpanzee competition is low, highlighting that competition, particularly from dominant species, suppresses the potential benefits of food abundance (Bryer et al. 2013; Lambert & Rothman 2015). The findings from this chapter challenge the assumption that increased food availability directly translates to better nutritional outcomes for smaller primates, emphasizing the need to account for interspecific competition when assessing ecological drivers of energy balance (Waser & Case, 1981; White, 2008). This insight aligns with the broader ecological literature, which recognizes the importance of competition in shaping

resource use and population dynamics in species-rich communities (Raubenheimer et al., 2009; Tilman, 1982).

In **Chapter 3**, the use of a remote-sensed Enhanced Vegetation Index (EVI) to predict food availability and energy balance introduces a new tool for the study of frugivorous primates in tropical rainforests. The study found that EVI lagged by 96 days provided the strongest predictor of urinary C-peptide (UCP) levels in red-tails, reflecting a negative relationship between vegetative greenness and net energy gain (van Schaik & Brockman, 2005). This finding supports the idea that periods of leaf flushing, as captured by EVI minima, precede fruiting events by about 2.5 months (van Schaik & Pfannes, 2009), which can be used to predict productive foraging opportunities for red-tailed monkeys (Emery Thompson & Knott, 2008). However, the scatter in individual energy balance data suggests that EVI alone may not fully account for energy fluctuations, pointing to the need for more integrative models that include additional environmental and physiological factors (Marshall & Wich, 2013; Slot & Winter, 2016). The chapter demonstrates the potential for remote-sensing technologies to enhance our understanding of the spatial and temporal patterns of food availability and their impacts on primate energetics.

Chapter 4 further explores the impact of interspecific competition by assessing the metabolic profiles of red-tailed monkeys across different competitive environments. Using a cluster analysis of metabolic biomarkers, I identified four distinct physical condition clusters, which varied based on the intensity of competition. Red-tail groups in habitats with more competitors were more frequently categorized into clusters characterized by prolonged energy deficits. These findings provide empirical support for the hypothesis that larger-bodied competitors universally suppress the energy balance of smaller primates, regardless of the number of competing species. This dynamic is rarely observed in competitive guilds (but

see Levi et al., 2020), and its physiological effect have never beed documented. Surprisingly, reproductive success did not correlate directly with physical condition nor with competitive pressure, indicating that red-tails may prioritize reproduction over maintaining optimal physical condition as an adaptive strategy under competitive stress (Harvey & Clutton-Brock, 1985). This chapter highlights the complex trade-offs that small-bodied primates must navigate between competition, energy mobilization, and reproductive success, adding a critical dimension to our understanding of primate life histories and their adaptive strategies.

The patterns observed across Chapters 2 and 4 reinforce the central role of competition in shaping energy balance and reproduction. In both chapters, the suppressive effects of competition from larger frugivores manifests in reduced energetic outcomes for the red-tails. The identification of metabolic clusters marked by prolonged energy deficits in competitive environments underscores the energetic costs small-bodied or subordinate primates face when competing with dominant species. This dynamic is further complicated by the trade-offs red-tails must navigate between immediate reproductive success and maintaining long-term physical condition. Together, these findings challenge prevailing assumptions within primate ecology and underscore the need for more nuanced models that integrate ecological, behavioral, and physiological factors to better predict foraging and energy allocation patterns (Emery Thompson et al., 2012; Raubenheimer et al., 2009). By combining remote-sensing tools, metabolic biomarkers, and detailed observations of competitive dynamics, this dissertation offers a novel approach to understanding primate behavior and energetics in complex ecological landscapes.

Finally, this work fills a crucial gap in the literature by addressing the physiological outcomes of interspecific competition, which have been underexplored in both ecological and primatological research (Schreier et al., 2009). By evaluating the interplay between

competition, food availability, and energy allocation, this dissertation provides valuable insights into the ecological constraints that shape primate behavior, community structure, and evolutionary strategies.

5.3 Bridging Gaps in Energy Theory

This research bridges the conceptual gaps between the Metabolic Theory of Ecology (MTE) and Dynamic Energy Budget (DEB) theory by integrating both frameworks to explain how small-bodied primates manage energy under competitive pressures. While MTE effectively explains how metabolic rates scale with body size (Brown et al., 2004), it overlooks the significant role that interspecific competition plays in energy allocation. The findings from this study challenge MTE's assumption that greater resource availability should always lead to increased energy gain (Raubenheimer et al., 2009). Red-tailed monkeys only benefit from increased fruit availability when competition from larger frugivores, such as chimpanzees, is low. This illustrates that competition fundamentally alters expected energy outcomes, revealing a shortcoming in MTE's reliance on resource abundance as a predictor. In contrast, DEB theory, which focuses on energy allocation across life functions like reproduction, maintenance, and growth, offers a more flexible explanation for the trade-offs red-tails make in competitive environments (Kooijman et al., 2004). The finding that red-tails prioritize reproduction over maintaining physical condition despite food stress aligns with DEB's predictions about organisms employing fast-paced life history strategies in response to competitive pressures (Harvey & Clutton-Brock, 1985). This points to the need to consider ecological interactions, such as competition, as crucial modifiers in energy models. DEB theory is better equipped to explain these complexities, as it accounts for the dynamic trade-offs between energy allocation and environmental fluctuations (Kooijman et

al., 2004). The work described in this dissertation bridges the static, size-based scaling of MTE with the adaptive, flexible perspective of DEB, providing a more comprehensive understanding of how small-bodied primates navigate ecological and social challenges in competitive environments.

5.4 The Role of Competition in Life History Theory

One of the central contributions of this dissertation is its focus on energy mobilization in small-bodied primates, particularly red-tailed monkeys, and the role competition plays in shaping their energy allocation strategies and life histories. Small-bodied species, with their higher metabolic rates and limited energy storage capacity, face distinct challenges in maintaining energy balance, especially in competitive, resource-scarce environments (McNab, 1980). This research highlights how competition from larger species, such as chimpanzees and mangabeys, significantly reduces access to preferred food resources, forcing red-tailed monkeys to adapt by increasing foraging efforts and exploiting less desirable foods, which often leads to energy deficits. Despite these challenges, red-tails adopt adaptive behaviors to cope with competition. However, these adaptations come at a cost, as their metabolic profiles reveal prolonged energy stress under intense competitive pressure (McGrosky & Pontzer, 2023).

A key insight of this work is that red-tailed monkeys may prioritize reproduction even when faced with energy deficits, aligning with life history strategies that favor immediate reproductive success over long-term physical maintenance (Harvey & Clutton-Brock 1985). The ability to reproduce under suboptimal conditions suggests that red-tails, like other small-bodied primates, exhibit reproductive behaviors that align more with the capital breeding end of the life history spectrum (Emery Thompson, 2013; Williams et al., 2017) compared to their larger competitors, like chimpanzees. They rely on accumulated energy reserves to

support reproduction during resource-scarce periods (Drent & Daan, 1980). This flexible energy allocation strategy allows red-tails to cope with the dual pressures of competition and reproduction, emphasizing the complex trade-offs they navigate in their ecological and social environments. The results underscore that competition plays a crucial role in shaping not only the foraging and energy use of small-bodied primates but also their reproductive strategies, contributing to a deeper understanding of how these primates manage energy in dynamic ecosystems.

5.5 Broader Significance in Primatology

This research makes important contributions to the field of primatology by highlighting the role of interspecific competition in shaping energy balance, survival, and reproductive strategies in small-bodied primates. The findings demonstrate that competition from larger-bodied frugivores, such as chimpanzees, disrupts the expected positive relationship between food availability and energy gain in red-tailed monkeys. This underscores the importance of considering social and ecological interactions, rather than just resource abundance, when examining energy outcomes in primate species. Additionally, the research shows that larger competitors have a universal suppressive effect on smaller species, further emphasizing the need to incorporate competitive dynamics when studying primate social behavior, feeding ecology, and life history strategies.

From a physiological perspective, this study offers novel insights into how competition affects primates at a deeper level by using biomarkers such as urinary C-peptide (UCP), triiodothyronine (T3), and nitrogen isotopes to track the metabolic consequences of competition. This biomarker approach provides a more detailed understanding of how competition influences energy use and reproductive investment in red-tailed monkeys, offering a framework for studying energy mobilization in other primates. Moreover, the

integration of remote-sensed productivity indices (such as the enhanced vegetation index, or EVI) as a predictor of food availability and energy balance introduces a valuable tool for long-term monitoring of primate populations, with significant implications for conservation efforts in the face of climate change and habitat fragmentation. Ultimately, this research highlights the adaptive flexibility of red-tailed monkeys, showing that even under energy stress, they prioritize reproduction, shedding light on the evolutionary pressures that shape primate life history strategies.

In summary, this dissertation offers exciting contributions to both ecology and primatology by highlighting the critical role of interspecific competition in shaping energy allocation, introducing new methodologies for studying primate energetics, and advancing our understanding of life history strategies in small-bodied primates. These findings underscore the importance of integrating physiological, ecological, and technological approaches to build a more complete picture of how primates—and potentially other species—navigate the complex and dynamic environments in which they live.

5.6 Improvements and Future Research Directions

While this research has provided valuable insights into the dynamics of energy mobilization and competition in small-bodied primates, there are areas for improvement and important directions for future research. One key limitation is the lack of long-term data, particularly for groups facing lower competitive pressures. Extending the study over longer periods for such groups would provide a deeper understanding of how energy allocation patterns fluctuate with environmental conditions and over time. For biomarker analysis, increasing the sample size would enhance statistical power and reveal more about intra-group variation in energy balance and reproductive success, especially under competitive stress. Additionally, accounting for differences in hormonal turnover rates might fine-tune

the use of a biomarker panel to evaluate behavior. For example, red-tails have particularly long transit times (i.e., the length of time from food consumption to excretion), so it is possible that individual foraging behavior might correspond with urinary biomarkers from that day, but fecal biomarkers from the following day.

Future research should also explore the effects of interspecific competition on the largest frugivores in this guild. Despite their superior ranking in this dominance hierarchy, chimpanzees also experience exploitation competition from the other frugivorous primates, yet the effects of these interactions are as poorly understood as they are for subordinate species. Additionally, other large primates, such as orangutans, gibbons, and spider monkeys, are also frugivorous competitors, but they play different roles than chimpanzees within their respective ecological communities. As the only habitual intraguild predators in the primate order, chimpanzees hold a unique role in their community, so they likely experience competition differently from other large and dominant frugivores. While it is important to assess the effect of interspecies competition on the smallest competitors, it is also important to measure these effects across the guild.

In this research, I focus on competition that red-tails experience from members of their primate feeding guild. However, other non-primate competitors, such as birds (hornbills, parrots, turacos), rodents (squirrels and rats), and viverrids (civets, and genets), and fruit bats, as well as other predators (golden cats and crowned hawk eagles) exist in this habitat. They must be considered too, albeit to a somewhat lesser degree, because their energetic and nutritional needs should overlap less with those of primates. Primates have unique gut morphologies that make their foraging patterns distinct from non-primates, even when contrasted with similar consumers (e.g., gorillas compared ungulates; Chivers, 1980). In addition, integrating additional environmental variables such as temperature and rainfall will

improve models of energy balance. Expanding the use of remote-sensing tools, like GPS tracking and alternative vegetation indices, could offer even greater insights into primate foraging behavior and movement patterns under competitive pressures. Finally, this research has significant conservation implications, as human-induced environmental changes intensify competition and disrupt resource availability. Understanding how competition affects primate survival and reproduction will be crucial for developing effective conservation strategies, particularly as habitats continue to fragment and food resources become less predictable.

The integration of biotic and abiotic factors- such as climate, resource availability, and seasonal changes- exerts a profound influence on the structure and behavior of primate communities and the competitive interactions within them. Studies of these characteristics have the potential to improve conservation strategies by identifying key factors that contribute to the resilience or vulnerability of primate populations in the face of environmental change. Primates are some of the most impacted taxa by human-induced environmental change (Estrada et al., 2017), so studying extant primate communities offers insights not only into how evolutionary histories, habitats, and species interactions shape species distributions but also into how modern impacts might shape or even re-construct future communities, which is crucial for species management and conservation. A deeper understanding of these dynamics is also essential for interpreting fossil primate communities, offering clues about the ecological pressures that shaped the evolution of modern primates, including humans.

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Appendix

6.1 Supplemental Information, Chapter II

6.1.1 Methods

To determine whether red-tailed monkey foraging patterns drive C-peptide levels (arrow B in Fig. 2.1) and whether feeding competition from chimpanzees affected this relationship, we evaluated how the time each group spent foraging on different food items (ripe and unripe fruit, fruit of unknown ripeness stage, flowers, young leaves, and insects) affected C-peptide values. We ran a single multilevel regression model (Bates et al., 2015; R Core Team, 2020) with the log-transformed C-peptide values as the response variable. The predictors included foraging on ripe and unripe fruit, uncategorized fruit (because it is impossible to determine the ripeness of some fruits before they are consumed), young leaves, and flowers, represented by the amount of time spent foraging on each food item as a proportion of all foraging observations per day. Chimpanzee competition, CHomp, was also included as a fixed effect and as an interaction term with foraging on ripe fruit. We initially included the effect of the amount of time spent foraging on insects as a predictor as well, but removed this variable because the model did not converge - likely because this term was collinear with some of the other predictors. We used month and red-tail group identity as crossed random effects (Rabe-Hesketh & Skrondal, 2008).

To determine whether the phenology of ripe fruit and competition from chimpanzees drive red-tail foraging patterns (arrow A in Fig. 2.1), we conducted a series of negative binomial generalized linear mixed models (*glmmTMB* package; Brooks et al., 2017; R Core Team, 2020). Each set of models included the daily count of foraging observations on a

particular food item as the outcome variable, and two fixed effect terms: a unique measure of ripe fruit phenology (TNC, quantity, or biomass in separate models), a measure of chimpanzee competition, and their interaction (Table S2.7). We used the total number of daily observations as an offset term and included month and red-tail group identity as crossed random effects (Rabe-Hesketh & Skrondal, 2008). Models of foraging on flowers (Table S2.7B) were run without 'group' as a random effect because the between-group variance was zero, causing singularity in the model. All models were type II negative binomial (B. Bolker, 2019; Ver Hoef & Boveng, 2007) to account for the zero-inflated nature of the foraging outcome variables (Ver Hoef & Jansen, 2007). I.e., If individuals are foraging on one type of food, they are inherently not foraging on others. Additionally, valuable food sources, such as ripe fruit, attract many group members to a single tree or grove, and many individuals feed on the same food type and not others. Lastly, in many of the group scans at least some individuals were not feeding on anything in particular, rather searching for food or traveling. For example, in 482 days out of the 750 group-days, zero individuals were observed foraging on unripe fruit (min = 0, mean = 2.1, max = 31.0 observations per day feeding on unripe fruit).

6.1.2 Results

The results of models using foraging behavior to predict C-peptide values in red-tailed monkeys show an unexpected pattern, opposite to what is predicted by phenology data. In these foraging models, red-tails seem to fare worse when CHomp is low (Table S2.6; Fig. S2.4). One possible explanation is that high CHomp forces monkeys to increase foraging effort on ripe fruit to gain energy, reflecting periods of positive energy balance that support reproductive efforts or energy storage (van Schaik & Brockman, 2005). In contrast, when

CHomp is low, they do not gain as much from foraging on ripe fruit, possibly due to lower quality fruit. In other words, red-tails only benefit from local resources by significantly increasing foraging effort on ripe fruit (potentially those not sought after by chimpanzees), and when CHomp is low, they do not benefit from increasing foraging on ripe fruit, perhaps because the ripe fruit that is available is of low nutritional value. Red-tails gain the most energy here when ripe fruit is abundant within their home range, which unsurprisingly might coincide with the abundance of specific fruit species preferred by, and which draw in chimpanzees–i.e., CHomp. This might explain some of the results of the models using fruit availability and competition to predict red-tail foraging (Table S2.7; Fig. S2.5, S2.6). However, this does not fully explain the pattern, as the highest foraging on ripe fruit coincides with high CHomp in some figures but not others. Another possibility is that they might be spending more time foraging on flowers and uncategorized fruits (Bryer, 2020; Lambert & Rothman, 2015), which are potentially unripe, or at least less sought after by chimpanzees, when CHomp is high, while also spending more time foraging on ripe fruit that chimpanzees are not pursuing.

6.1.3 Figures

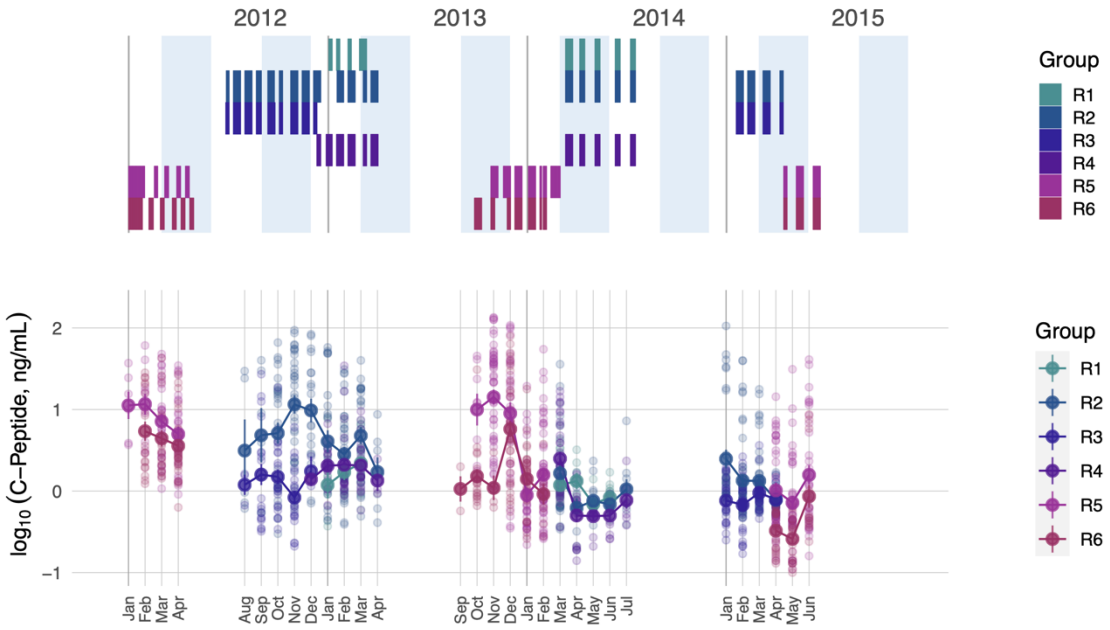

Figure S2.1. Observation Periods, Data Collection, and Mean C-peptide. (a) Periods in which six groups of red-tailed monkeys were observed and in which urine samples were collected at the Ngogo site. Light blue bars indicate typical rainy seasons (March-May and September-November). **(b)** Mean C-peptide values per group and month; error bars indicate the standard error of the mean. Light points indicate individual C-peptide values per urine sample.

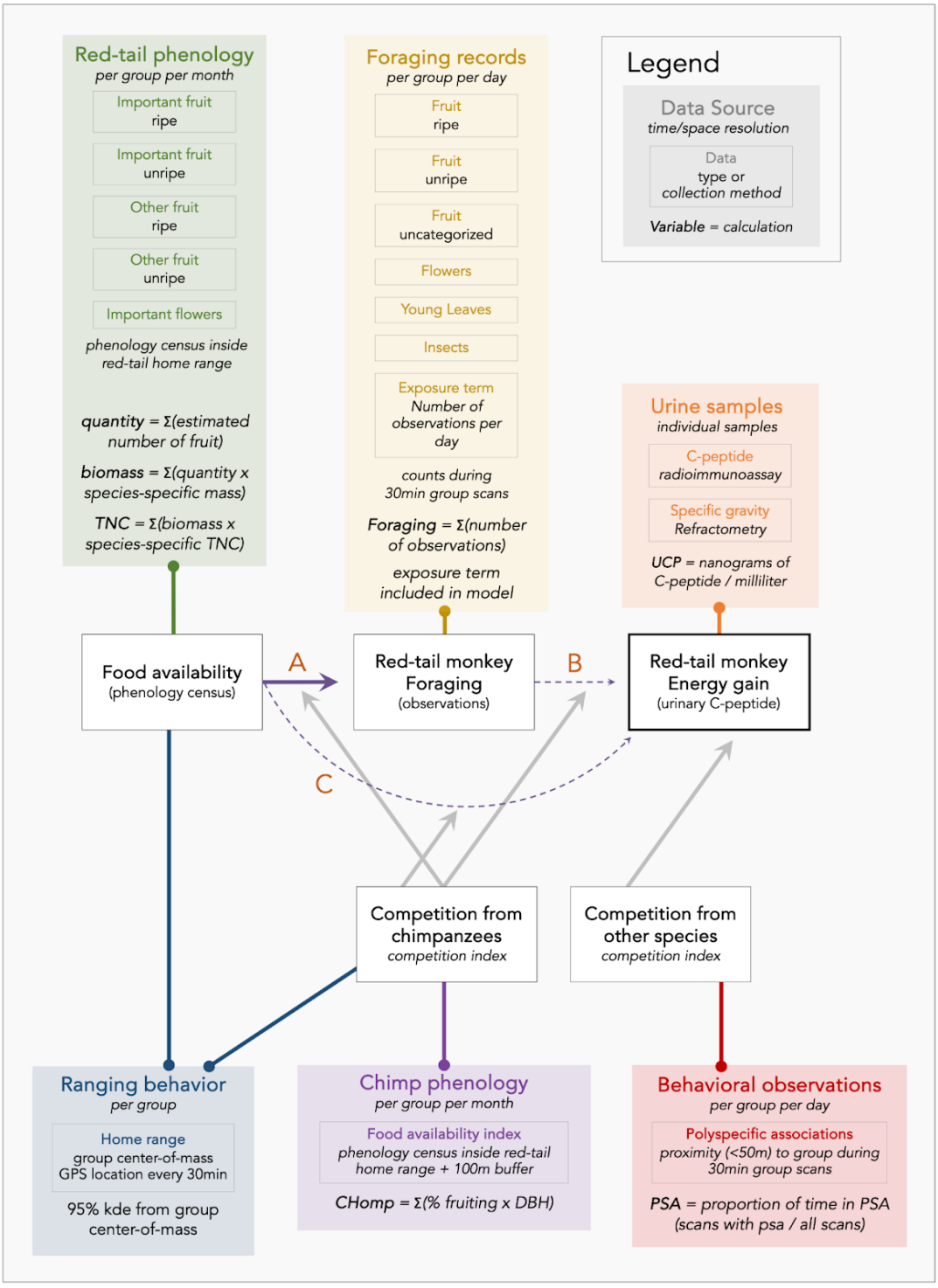

Figure S2.2. Data Collection and Aggregation. Schematic representation of the source and collection methods of all data included in this study, corresponding to each object of analysis. Purple and gray lines represent positive and negative relationships, respectively. Thick solid and thin dashed lines represent significant and insignificant relationships, respectively (see Fig. 2.1; Tables S2.4, S2.6, S2.7).

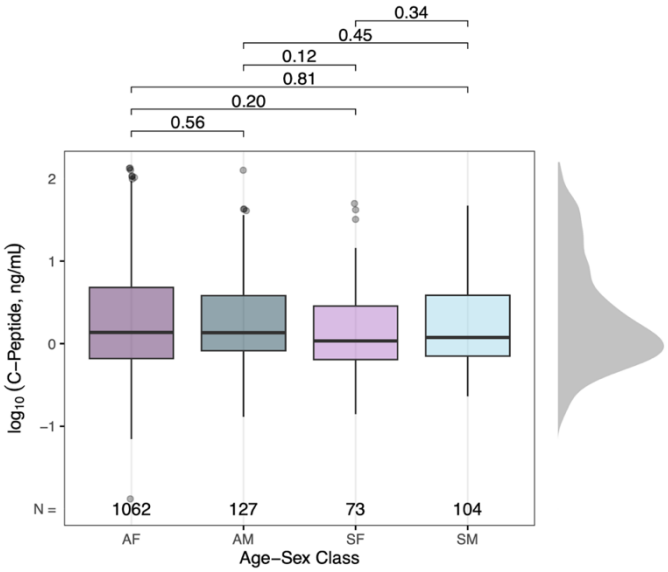

Figure S2.3. Age-Sex Class Comparison of C-peptide. Red-tailed monkey C-peptide values (log10-transformed; in ng/mL) per age-sex class (AF = adult female, AM = adult male, SF = sub-adult female, SM = sub-adult male; N = 1,366 urine samples) at the Ngogo site in Kibale National Park, Uganda. Boxplots indicate the 25th, median, and 75th percentiles; whiskers indicate values ≤1.5 times the interquartile range; and jittered points are statistical outliers. Density plot (right side) includes the C-peptide values of all samples in the study. P-values above the horizontal brackets indicate Wilcoxon pairwise comparisons among classes.

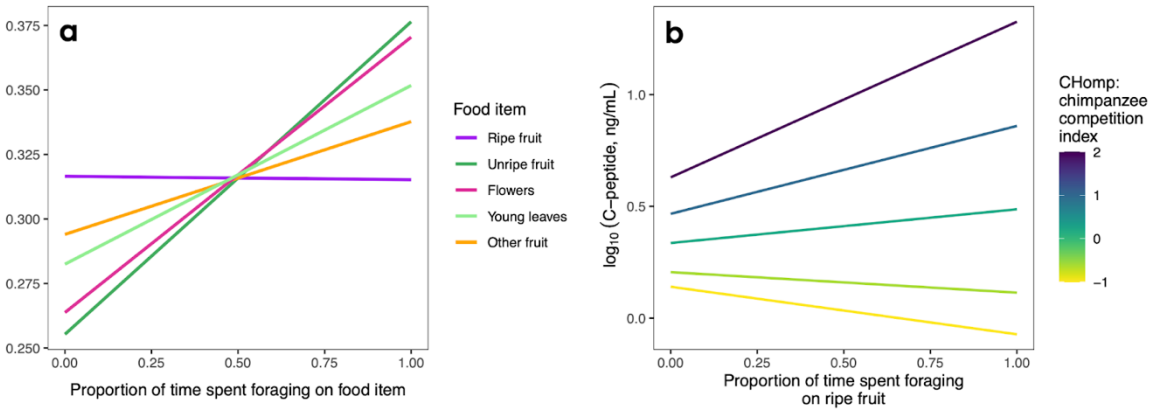

Figure S2.4. Using Red-Tail Foraging and Chimpanzee Competition to Predict Red-Tail C-Peptide. Red-tailed monkey C-peptide levels as a function of the amount of time spent foraging on different food items per day. Foraging on all fruit types, flowers, young leaves, and other plant parts were included as fixed effects in a single inclusive multilevel regression model (Table S2.6). Lines indicate modeled values of C-peptide. a) C-peptide predicted by foraging on all food types. b) C-peptide predicted by an interaction between foraging on ripe fruit and CHomp, a chimpanzee competition index.

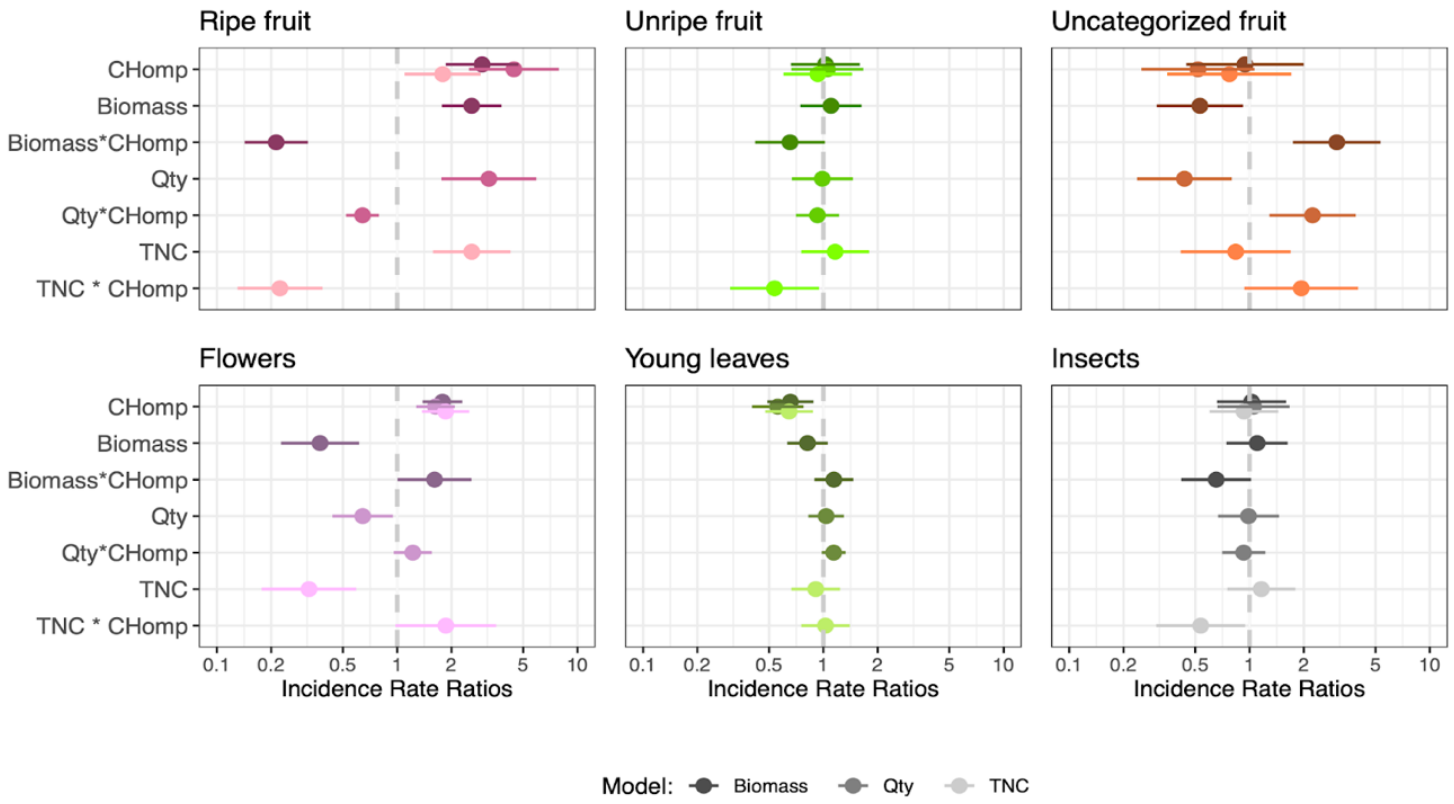

Figure S2.5. Using Food Availability and Chimpanzee Competition to Predict Red-Tail Foraging. Forest plots depicting the relationship between the availability of preferred ripe fruit within the red-tail group home ranges and their foraging behavior on different food types, using multilevel negative binomial models (as detailed in Table S2.7). Each plot compares three food availability measures—'Biomass' (kg, dark shading), 'Quantity' (Qty; intermediate shading), and 'TNC' (total nonstructural carbohydrates in grams, light shading)—used in three models, and its effect on the proportion of time spent feeding on one of six food types (ripe fruit, unripe fruit, uncategorized fruit, flowers, young leaves, and insects). CHomp, a chimpanzee competition index, is included as an independent variable and as an interaction with the food availability measure in each model.

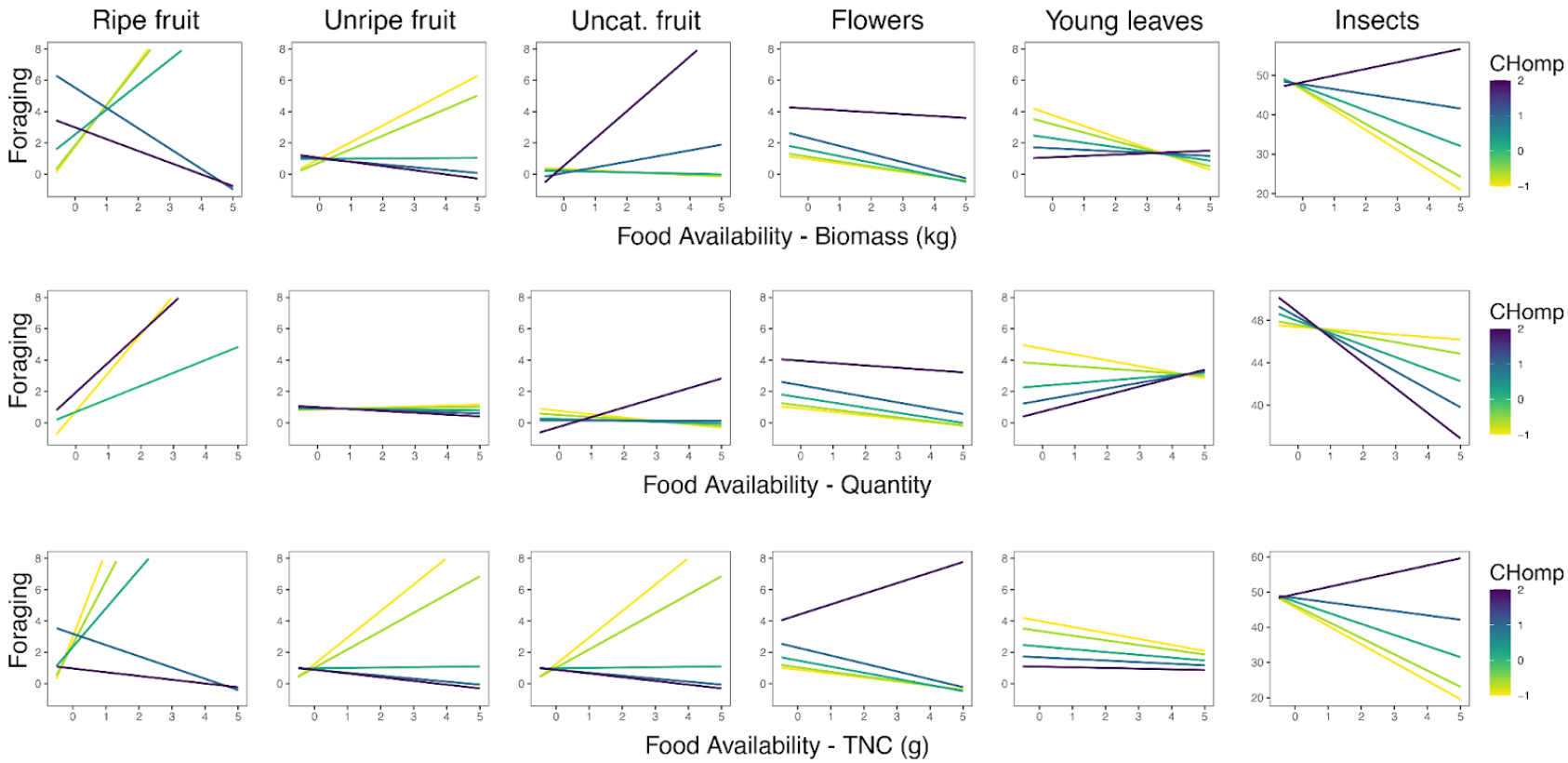

Figure S2.6. Using Food Availability and Chimpanzee Competition to Predict Red-Tail Foraging. Red-tailed monkey foraging as a function of food availability and feeding competition from chimpanzees (CHomp). Rows show food availability measured as biomass (kg), quantity, and total nonstructural carbohydrates (TNC; g). Each column indicates foraging on a different type of food item (ripe fruit, unripe fruit, flowers, young leaves, and insects). Lines indicate negative binomial model-fitted values for time spent foraging (observations per day). Light (yellow) lines represent low values of CHomp in each panel, and dark lines (purple) represent high values. The total number of observations per day was included in the model as an exposure variable.

6.1.4 Tables

Table S2.1. Multilevel Linear Regression Models Used to Evaluate Competition and C-Peptide. Structure of eight multilevel linear regression models used to evaluate the effects of fruit availability and chimpanzee competition on red-tailed monkey urinary C-peptide levels. Each model contains at least one measure of red-tailed monkey fruit availability (from the Ngogo Monkey Project plant phenology census [Red-tails]) and an interaction term with chimpanzee competition (from the Ngogo Chimpanzee Project plant phenology census [Chimpanzees]). Food availability is measured within the scope of the red-tailed monkey home range, including a 100 m buffer around the outer periphery. Important foods are plant species that constitute ≥10% of the observed plant diet consumed by at least one red-tail group in at least one observation period, and unimportant are all other species. Flowers are measured from all angiosperms. Polyspecific associations (PSA) are the proportion of time a group spent in association with other primate species (MY = grey-cheeked mangabeys; BL = blue monkeys). "○" are variables included in the models as main effects, and "◉" are variables included in the models as part of an interaction with another variable with the same marker. An initial set of models, consisting of a null model and six fruit models, were evaluated to determine the confidence set of best-fit models to predict C-peptide values (see Table S2.3); the best-fit model (model 1, TNC – Ripe) was then expanded to include polyspecific associations (model 7, Best fit + PSA).

Data:		*Red-tails*							*Chimpanzees*
		important foods		unimportant foods		flowers	PSA		competition index
Models:	Number	Ripe	Unripe	Ripe	Unripe		*MY*	*BL*	
Null	0								
TNC	1	◉		○		○			◉
	2		◉		○	○			◉
Quantity	3	◉		○		○			◉
	4		◉		○	○			◉
Biomass	5	◉		○		○			◉
	6		◉		○	○			◉
Best-fit model + PSA	7	◉		○		○	○	○	◉

Table S2.2. Using Plant Phenology and Chimpanzee Competition to Predict Red-Tailed Monkey C-peptide. Multilevel linear models of the relationship between fruit availability and energy balance (C-peptide, ng/mL). Fruit is measured as total non-structural carbohydrates (TNC; g), quantity of food items, and biomass (kg). Fruit availability for red-tail monkeys is tracked in the monthly red-tail phenology census (where 'important' and 'unimportant' fruiting species refer to frequently or less-often consumed plant species). Feeding competition from chimpanzees (CHomp) is measured as the availability of important foods for chimpanzees within the red-tail home range. Urinary C-peptide values are log10-transformed. N = 1,228 urine samples.

		Ripe Fruit			Unripe Fruit		
	Predictors	*β*	*95% CI*	*P-value*	*β*	*95% CI*	*P-value*
TNC (g)	Intercept	0.34	0.07, 0.61	**0.015**	0.31	0.05, 0.57	**0.020**
	Flowers	0.03	-0.02, 0.08	0.251	0.01	-0.04, 0.06	0.611
	Unimportant red-tail foods	-0.04	-0.11, 0.03	0.305	-	-	-
	Important red-tail foods	0.04	-0.07, 0.15	0.499	-0.04	-0.11, 0.04	0.328
	CHomp	0.22	0.11, 0.33	**<0.001**	0.25	0.15, 0.35	**<0.001**
	Interaction (important x CHomp)	-0.17	-0.29, -0.05	**<0.005**	0.01	-0.05, 0.07	0.715
	Random Effects: σ^2 / τ_{00} / ICC		0.24 / 0.10, 0.09 / 0.45			0.24 / 0.08, 0.09 / 0.41	
	Model Parameters: σ^2_f / R^2_M / R^2_C / **AIC**		0.06 / 0.12 / 0.52 / **1886.8**			0.06 / 0.12 / 0.48 / **1899.5**	
Quantity	Intercept	0.33	0.06, 0.59	**0.017**	0.30	0.02, 0.58	**0.033**
	Flowers	0.01	-0.05, 0.07	0.733	0.00	-0.06, 0.06	0.925
	Unimportant red-tail foods	0.00	-0.09, 0.09	0.957	0.02	-0.09, 0.13	0.723
	Important red-tail foods	0.07	-0.02, 0.16	0.149	-0.03	-0.09, 0.04	0.439
	CHomp	0.25	0.14, 0.36	**<0.001**	0.24	0.13, 0.35	**<0.001**
	Interaction (important x CHomp)	0.01	-0.05, 0.08	0.734	0.03	-0.03, 0.10	0.265
	Random Effects: σ^2 / τ_{00} / ICC		0.24 / 0.09, 0.09 / 0.43			0.24 / 0.10, 0.10 / 0.44	
	Model Parameters: σ^2_f / R^2_M / R^2_C / **AIC**		0.06 / 0.12 / 0.50 / **1904.6**			0.05 / 0.11 / 0.50 / **1905.3**	
Biomass (kg)	Intercept	0.34	0.06, 0.61	**0.017**	0.30	0.03, 0.56	**0.028**
	Flowers	0.03	-0.02, 0.08	0.244	0.02	-0.03, 0.06	0.510
	Unimportant red-tail foods	-0.02	-0.10, 0.05	0.492	0.06	-0.01, 0.14	0.104
	Important red-tail foods	0.01	-0.09, 0.11	0.881	-0.11	-0.21, -0.02	**0.019**
	CHomp	0.25	0.15, 0.36	**<0.001**	0.27	0.17, 0.37	**<0.001**
	Interaction (important x CHomp)	-0.13	-0.24, -0.03	**<0.001**	-0.03	-0.09, 0.03	0.357
	Random Effects: σ^2 / τ_{00} / ICC		0.24 / 0.10, 0.10 / 0.45			0.25 / 0.06, 0.09 / 0.39	
	Model Parameters: σ^2_f / R^2_M / R^2_C / **AIC**		0.06 / 0.13 / 0.52 / **1889.2**			0.07 / 0.16 / 0.49 / **1901.2**	

IRR = Incidence rate ratio; σ^2 = Mean random effects variance; τ_{00} = Random intercept variance: observation month, group; σ^2_f = Fixed effects variance; R^2_M / R^2_C = Marginal R^2 / Conditional R^2; AIC = Akaike information criterion.

Table S2.3. Akaike Information Criterion (AIC) Table. Information-theoretic comparison of multilevel linear regression models shown in Table S2.1 (Burnham and Anderson 2002). N = 1,228 urine samples for all models. Only one model (model 1) fell within the confidence set of best-fit models, indicated in bold font. This model is 3.3 times better at predicting C-peptide values than the next-best model (model 5).

Model	RSS	K	AICc	Δ_i	ω_i
0 Null	293.37	5	1894.45	7.50	0.02
1 TNC - Ripe	**284.05**	**10**	**1886.95**	0.00	**0.75**
2 TNC - Unripe	290.16	9	1899.67	12.72	< 0.01
3 Quantity - Ripe	289.49	10	1904.82	17.87	< 0.01
4 Quantity - Unripe	289.00	10	1905.48	18.53	< 0.01
5 Biomass - Ripe	284.54	10	1889.34	2.39	0.23
6 Biomass - Unripe	291.40	10	1901.37	14.42	< 0.01

Table S2.4. Expanded Best-Fit Model of Plant Phenology and Chimpanzee Competition to Predict Red-Tailed Monkey C-peptide Levels. Best-fit model (model 1, TNC-ripe from Table S2.3) expanded with polyspecific association (PSA) terms. The response variable is log-transformed values of urinary C-peptide (ng/mL); N = 1,228 urine samples. TNC is the amount of total nonstructural carbohydrates (g) of important and unimportant fruits and flowers for red-tails within their home range. CHomp is a chimpanzee competition index estimated within each red-tailed monkey home range. PSA is the proportion of time a group spent in association with other primate species.

Predictors	β	95% CI	P-value
Intercept	0.39	0.09, 0.68	**0.010**
TNC Flowers in red-tail diet	0.02	-0.02, 0.07	0.315
TNC Unimportant ripe fruit in red-tail diet	-0.05	-0.12, 0.03	0.207
TNC Important ripe fruit in red-tail diet	0.05	-0.06, 0.17	0.385
CHomp	0.25	0.14, 0.37	**<0.001**
Interaction (TNC Important ripe fruit x CHomp)	-0.17	-0.29, -0.05	**0.005**
PSA mangabeys	-0.20	-0.32, -0.09	**0.001**
PSA blue monkeys	0.13	-0.13, 0.38	0.341
Random Effects: σ^2 / τ_{00} / ICC		0.24 / 0.11, 0.11 / 0.48	
Model Parameters: σ^2_f / R^2_M / R^2_C		0.07 / 0.14 / 0.55	

Table S2.5. Using Red-Tail Foraging and Chimpanzee Competition to Predict Red-Tail C-Peptide. Linear mixed-effects regression model indicates the effect of the proportion of time red-tails spent foraging on ripe and unripe fruit, flowers, and young leaves on urinary C-peptide values. CHomp is the chimpanzee competition index, estimated within each red-tailed monkey home range per month. N = 1,221 urine samples.

Predictors	β	**95% CI**	**P-value**
Intercept	0.26	-0.11 – 0.62	0.165
CHomp	0.16	0.04 – 0.28	**0.007**
Red-tailed monkey foraging on important ripe fruits	0.09	-0.17 – 0.35	0.494
Interaction (important ripe fruits x CHomp)	0.30	0.16 – 0.45	**<0.001**
Red-tailed monkey foraging on important unripe fruits	0.12	-0.19 – 0.43	0.442
on uncategorized fruits	0.04	-0.23 – 0.32	0.757
on flowers	0.11	-0.19 – 0.40	0.474
on young leaves	0.07	-0.24 – 0.38	0.659
Random Effects: σ^2 / τ_{00} / ICC		0.26 / 0.09, 0.11 / 0.44	
Model Parameters: σ^2_f / R^2_M / R^2_C		0.05 / 0.10 / 0.50	

Table S2.7. Using Food Availability and Chimpanzee Competition to Predict Red-Tail Foraging. Multilevel negative binomial models of red-tailed monkey foraging behavior on specific food items (**A** = ripe and unripe fruit, **B** = uncategorized fruit and flowers, **C** = young leaves and insects) as a function of the availability of all fruit available in the home range and feeding competition from chimpanzees (CHomp). N = 750 daily group foraging records. The flower models were run without group as a random effect because the variance (τ_{00}) was zero, causing singularity in the model.

A	**Outcome = foraging on:**	**Ripe Fruit**				**Unripe Fruit**			
	Predictors	IRR	*95% CI*	*Z-score*	*P-value*	IRR	*95% CI*	*Z-score*	*P-value*
TNC (g)	Intercept	0.03	0.01, 0.08	-6.14	**<0.001**	0.01	0.01, 0.03	-13.77	**<0.001**
	TNC of fruit	2.59	1.58, 4.25	3.77	**<0.001**	1.16	0.75, 1.79	0.68	0.498
	CHomp	1.79	1.10, 2.91	2.34	**0.019**	0.93	0.60, 1.44	-0.32	0.752
	Interaction	0.22	0.13, 0.38	-5.41	**<0.001**	0.54	0.30, 0.95	-2.15	**0.031**
	Random Effects: σ^2 / τ_{00} / ICC			3.63 / 5.55, 1.06 / 0.65				4.42 / 1.13, 0.29 / 0.24	
	Model Parameters: σ^2_f / R^2_M / R^2_C			1.61 / 0.14 / 0.69				0.17 / 0.03 / 0.27	
	AIC			3968.4					**2334.4**
Quantity	Intercept	0.02	0.00, 0.08	-5.22	**<0.001**	0.01	0.01, 0.02	-12.97	**<0.001**
	Quantity of fruit	3.22	1.76, 5.91	3.78	**<0.001**	0.99	0.67, 1.46	-0.07	0.948
	CHomp	4.44	2.50, 7.88	5.09	**<0.001**	1.05	0.66, 1.67	0.22	0.827
	Interaction	0.64	0.52, 0.79	-4.13	**<0.001**	0.93	0.70, 1.22	-0.53	0.594
	Random Effects: σ^2 / τ_{00} / ICC			3.63 / 10.63, 1.77/ 0.77				4.42 / 1.28, 0.37 / 0.27	
	Model Parameters: σ^2_f / R^2_M / R^2_C			2.94 / 0.16 / 0.81				0.01 / 0.00 / 0.27	
	AIC			3974.5					2340.0
Biomass (kg)	Intercept	0.03	0.01, 0.10	-5.37	**<0.001**	0.01	0.01, 0.03	-13.41	**<0.001**
	Biomass of fruit	2.59	1.77, 3.79	4.90	**<0.001**	1.10	0.75, 1.63	0.49	0.626
	CHomp	2.96	1.86, 4.70	4.59	**<0.001**	1.03	0.66, 1.60	0.12	0.908
	Interaction	0.21	0.14, 0.32	-7.49	**<0.001**	0.65	0.42, 1.02	-1.87	0.062
	Random Effects: σ^2 / τ_{00} / ICC			3.63 / 6.43, 1.54 / 0.69				4.49 / 1.21, 0.31 / 0.25	
	Model Parameters: σ^2_f / R^2_M / R^2_C			2.42 / 0.17 / 0.74				0.09 / 0.02 / 0.27	
	AIC			**3941.7**					2336.2

B	Outcome = foraging on:	Uncategorized Fruit				Flowers			
	Predictors	IRR	*95% CI*	*Z-score*	*P-value*	IRR	*95% CI*	*Z-score*	*P-value*
TNC (g)	Intercept	0	0.00, 0.07	-3.86	**<0.001**	0.02	0.01, 0.03	-12.98	**<0.001**
	TNC of fruit	0.84	0.41, 1.69	-0.50	0.621	0.32	0.18, 0.59	-3.66	**<0.001**
	CHomp	0.77	0.35, 1.71	-0.64	0.524	1.86	1.37, 2.51	4.01	**<0.001**
	Interaction	1.94	0.94, 4.01	1.78	0.075	1.86	0.98, 3.54	1.89	0.058
	Random Effects: σ^2 / τ_{00} / ICC			5.44 / 9.26, 9.49 / 0.78				3.97 / 3.23, - / 0.45	
	Model Parameters: σ^2_f / R^2_M / R^2_C			0.26 / 0.01 / 0.78				1.19 / 0.14 / 0.53	
	AIC				3113.7				2649.9
Quantity	Intercept	0	0.00, 0.08	-3.59	**<0.001**	0.02	0.01, 0.04	-10.81	**<0.001**
	Quantity of fruit	0.44	0.24, 0.80	-2.69	**0.007**	0.64	0.44, 0.95	-2.23	**0.026**
	CHomp	0.52	0.25, 1.07	-1.79	0.074	1.63	1.27, 2.09	3.87	**<0.001**
	Interaction	2.24	1.29, 3.88	2.86	**0.004**	1.22	0.96, 1.56	1.61	0.107
	Random Effects: σ^2 / τ_{00} / ICC			5.44 / 12.71, 11.03 / 0.81				3.97 / 4.52, - / 0.53	
	Model Parameters: σ^2_f / R^2_M / R^2_C			1.43 / 0.05 / 0.82				0.39 / 0.04 / 0.55	
	AIC				**3102.9**				2656.6
Biomass (kg)	Intercept	0	0.00, 0.07	-3.62	**<0.001**	0.02	0.01, 0.03	-13.31	**<0.001**
	Biomass of fruit	0.53	0.31, 0.92	-2.25	**0.024**	0.37	0.23, 0.61	-3.87	**<0.001**
	CHomp	0.94	0.44, 2.00	-0.15	0.879	1.78	1.38, 2.30	4.46	**<0.001**
	Interaction	3.05	1.74, 5.33	3.91	**<0.001**	1.61	1.00, 2.59	1.97	**0.048**
	Random Effects: σ^2 / τ_{00} / ICC			5.44 / 10.6, 12.4 / 0.81				3.97 / 3.05, - / 0.43	
	Model Parameters: σ^2_f / R^2_M / R^2_C			0.63 / 0.02 / 0.81				0.97 / 0.12 / 0.50	
	AIC				3104.5				**2648.4**

C	Outcome = foraging on:	Young Leaves				Insects			
	Predictors	IRR	*95% CI*	*Z-score*	*P-value*	IRR	*95% CI*	*Z-score*	*P-value*
TNC (g)	Intercept	0.04	0.02, 0.07	-10.62	**<0.001**	0.66	0.59, 0.73	-8.1	**<0.001**
	TNC of fruit	0.91	0.66, 1.24	-0.61	0.541	0.91	0.88, 0.95	-4.59	**<0.001**
	CHomp	0.65	0.48, 0.88	-2.81	**0.005**	1.02	0.98, 1.06	1.14	0.254
	Interaction	1.03	0.75, 1.40	0.17	0.867	1.07	1.03, 1.11	3.21	**0.001**
	Random Effects: σ^2 / τ_{00} / ICC			3.42 / 0.85, 0.41 / 0.27				0.92 / 0.01, 0.01 / 0.03	
	Model Parameters: σ^2_f / R^2_M / R^2_C			0.16 / 0.03 / 0.30				0.00 / 0.01 / 0.03	
	AIC				3322.9				5332.4
Quantity	Intercept	0.04	0.02, 0.07	-10.11	**<0.001**	0.66	0.60, 0.74	-7.93	**<0.001**
	Quantity of fruit	1.04	0.83, 1.30	0.30	0.761	0.98	0.95, 1.01	-1.42	0.155
	CHomp	0.56	0.40, 0.78	-3.46	**0.001**	1.01	0.97, 1.05	0.47	0.637
	Interaction	1.14	0.98, 1.33	1.70	0.09	0.98	0.96, 1.00	-1.55	0.122
	Random Effects: σ^2 / τ_{00} / ICC			3.42 / 0.85, 0.47 / 0.28				0.92 / 0.01, 0.01 / 0.03	
	Model Parameters: σ^2_f / R^2_M / R^2_C			0.26 / 0.05 / 0.32				0.00 / 0.00 / 0.03	
	AIC				**3320.8**				5354.4
Biomass (kg)	Intercept	0.04	0.02, 0.07	-10.62	**<0.001**	0.66	0.59, 0.73	-7.79	**<0.001**
	Biomass of fruit	0.82	0.63, 1.06	-1.53	0.125	0.92	0.89, 0.95	-5.12	**<0.001**
	CHomp	0.66	0.49, 0.88	-2.80	**0.005**	1.01	0.97, 1.05	0.61	0.544
	Interaction	1.14	0.89, 1.47	1.06	0.288	1.06	1.03, 1.10	3.58	**<0.001**
	Random Effects: σ^2 / τ_{00} / ICC			3.42 / 0.87, 0.42 / 0.27				0.92 / 0.01, 0.02 / 0.03	
	Model Parameters: σ^2_f / R^2_M / R^2_C			0.20 / 0.04 / 0.30				0.00 / 0.01 / 0.03	
	AIC				3321.3				**5328.9**

IRR = Incidence rate ratio; σ^2 = Mean random effects variance; τ_{00} = Random intercept variance: observation month, group; σ^2_f = Fixed effects variance; R^2_M / R^2_C = Marginal R^2 / Conditional R^2; AIC = Akaike information criterion

Table S2.8. Species Included in Plant Phenology Censuses. List of plant species recorded in the red-tail and chimpanzee phenology censuses. Important foods for red-tailed monkeys were defined as those that constituted ≥10% of the monthly diet of at least one group in any observation period. All plant species recorded in the chimpanzee census were important foods for chimpanzees.

	Species (*N = 76 species; overlap of 30 species*)	**Important for red-tails (*N* = 30)**	**Red-tail (*N = 68*)**	**Chimpanzee (*N = 38*)**
1	*Aeglopsis eggelingii*		x	
2	*Aframomum*		x	
3	*Allophylus spp.*		x	
4	*Aningeria altissima*		x	x
5	*Aphania senegalensis*	Y	x	x
6	*Balanites wilsoniana*		x	
7	*Blighia unijugata*		x	x
8	*Bosqueia phoberos*	Y	x	x
9	*Casearia runssorica*	Y	x	
10	*Cecropia*		x	
11	*Celtis africana*			x
12	*Celtis durandii*	Y	x	x
13	*Chaetachme aristata*		x	
14	*Chrysophyllum albidum*	Y	x	x
15	*Cissus petiolata*	Y	x	
16	*Clerodendron capitatum*		x	
17	*Coffea eugenioides*		x	
18	*Cordia africana (abyssinica)*		x	
19	*Cordia millenii*		x	x
20	*Dasylepis eggelingii*	Y	x	x
21	*Diospyros abyssinica*	Y	x	x
22	*Dovyalis macrocalyx*		x	

23	*Elaeodendron buchananii*		x	x
24	*Erythrina abyssinica*		x	
25	*Erythrina exelsa*			x
26	*Euadenia eminens (alimensis)*		x	
27	*Ficus brachylepis*	Y	x	x
28	*Ficus capensis*			x
29	*Ficus cyathistipula*		x	x
30	*Ficus dawei*	Y	x	x
31	*Ficus exasperata*		x	x
32	*Ficus mucuso*	Y	x	x
33	*Ficus natalensis*	Y	x	x
34	*Ficus vallis-choudae*			x
35	*Funtumia africana*		x	
36	*Harrisonia abyssinica*		x	
37	*Leptonychia mildbraedii*		x	
38	*Lindackeria*		x	
39	*Linociera johnsonii*			x
40	*Macaranga schweinfurthii*		x	
41	*Maesa lanofolato*	Y	x	
42	*Milletia dura*		x	x
43	*Mimusops bagshawei*	Y	x	x
44	*Monodora myristica*	Y	x	x
45	*Morus lactea*	Y	x	x
46	*Neoboutonia macrocalyx*		x	
47	*Okina*		x	
48	*Oncoba*		x	
49	*Oxyanthus latifolia*		x	

50	*Pancovia turbinata*			x
51	*Parinari excelsa (holstii)*		x	
52	*Parkia*		x	
53	*Paullinia pinnata*	Y	x	
54	*Piptadeniastrum (Piptadenia) africanum*		x	
55	*Pleiocarpa pycnantha*		x	
56	*Premna angolensis*			x
57	*Pseudospondias microcarpa*	Y	x	x
58	*Pterygota mildbraedii*		x	x
59	*Randia urcelliformis*	Y	x	x
60	*Rauvolfia oxyphylla*	Y	x	
61	*Rothmannia (Randia) longiflora*		x	
62	*Rothmannia (Randia) whitfieldii*		x	
63	*Salacia elegans*	Y	x	
64	*Spathodea campanulata*			x
65	*Strombosia scheffleri*		x	
66	*Syrpheonema fasciculatum*	Y	x	
67	*Tabernaemontana holstii*	Y	x	x
68	*Tarenna pavettoides*	Y	x	
69	*Teclea nobilis*	Y	x	x
70	*Toddalia asiatica*	Y	x	
71	*Treculia africana*		x	x
72	*Trichilia drageana*		x	x
73	*Uvariopsis congensis*	Y	x	x
74	*Vangueria apiculata*	Y	x	
75	*Warburgia ugandensis*	Y	x	x
76	*Zanha golungensis*	Y	x	x

6.2 SUPPLEMENTAL INFORMATION, CHAPTER III

6.2.1 Bayesian Hierarchical Model Approach

In this analysis, we aimed to investigate the predictive relationship between vegetation indices (EVI) and urinary C-peptide (UCP) levels using a Bayesian hierarchical framework. Based on *a priori* ecological evidence that fruiting patterns in African rainforests correlate with vegetative flushing 2.5 months prior, but which can extend up to 4 months (van Schaik & Pfannes, 2009), we focused on the 80-day lag as a potential predictor of UCP (five 16-day cycles ago, or *Period –5*). However, to account for potential variability in the timing of fruiting events, we extended the analysis to consider lags of 64, 80, 96, and 112 days. These time points were chosen to represent a range of possible correlations between environmental conditions and energy balance, spanning from approximately two to four months before UCP measurements.

6.2.2 Selection of EVI Metrics

We explored three EVI metrics as predictors of UCP:

Mean EVI: Represents the average vegetation index across the home range.

Maximum EVI: Captures the highest EVI value, under the assumption that the densest vegetation patches could be the most influential in determining food availability.

Weighted Sum EVI: Reflects the overall productivity of the home range, accounting for the sum of EVI values weighted by the area of each pixel, which could better represent the entire home range's productivity rather than relying on a single peak.

6.2.3 Bayesian Model Structure

The Bayesian models were implemented using a hierarchical structure, with UCP as the response variable and EVI (mean, max, or weighted sum) as the fixed effect. Group and observation period were included as random intercepts to account for between-group variation and temporal effects, respectively. The model structure can be summarized as:

UCP_{ij}: This is the response variable (log_{10}-transformed mean UCP) for $group_i$ at observation $period_j$. It represents the energy balance (as measured by UCP) for a particular group and time.

EVI_{ij}: This is the fixed effect of the EVI (mean, max, or weighted sum) for $group_i$ at observation $period_j$. It's the predictor variable, representing the vegetation index (EVI) value at a certain lag for that group and time period.

(1 | $group_i$): This term represents a random intercept for the different groups (social groups of the monkeys). It accounts for the variability in UCP across different groups, allowing each group to have its own baseline level of UCP that can differ from other groups.

(1 | observation $period_j$): This term represents a random intercept for the observation period. It allows each observation period to have its own baseline UCP level, accounting for any time-specific factors or temporal variability that might affect UCP measurements across all groups, where EVI_{ij} represents the lagged EVI predictor for $group_i$ at observation $period_j$, and UCP_{ij} represents the log-transformed mean UCP.

6.2.4 Model Comparison Using Leave-One-Out Cross-Validation (LOO)

To compare the predictive performance of each lag and EVI metric, we employed Leave-One-Out Cross-Validation (LOO), a method that evaluates the out-of-sample

predictive ability of each model. The LOO results are presented in terms of the expected log predictive density difference (elpd_diff) between models (Fig. S3.3), with lower elpd_diff values indicating worse predictive performance relative to the best-performing model (which is assigned elpd_diff = 0).

6.2.5 Results Summary

Mean EVI: The model with a 96-day lag provided the best predictive performance (elpd_diff = 0), followed closely by the 64-day lag (elpd_diff = -0.3; Fig. S3.4). Models with lags of 80 and 112 days performed worse, with elpd_diff values of -3.4 and -3.2, respectively.

Max EVI: The 64-day lag was the strongest predictor (elpd_diff = 0), with the 96-day lag only slightly worse (elpd_diff = -0.4). The 80-day and 112-day lags performed similarly, with minor differences.

Weighted Sum EVI: The 64-day lag again showed the best performance (elpd_diff = 0), while the 96-day lag was moderately worse (elpd_diff = -1.8). Larger performance drops were observed for the 80- and 112-day lags (elpd_diff = -3.4 and -3.1, respectively).

While the 96-day lag for mean EVI emerged as the strongest overall predictor of UCP, the results for max and weighted sum EVI suggested that a 64-day lag may also be relevant. However, the differences in predictive performance between lags and EVI metrics were not large, leaving the results somewhat inconclusive. The Bayesian analysis, while useful in exploring these relationships, suggests that further refinement may be necessary, especially with respect to capturing potential variations in lag times across different ecological conditions. All model results and detailed comparisons are provided in this supplemental material for further exploration.

6.2.6 Figures

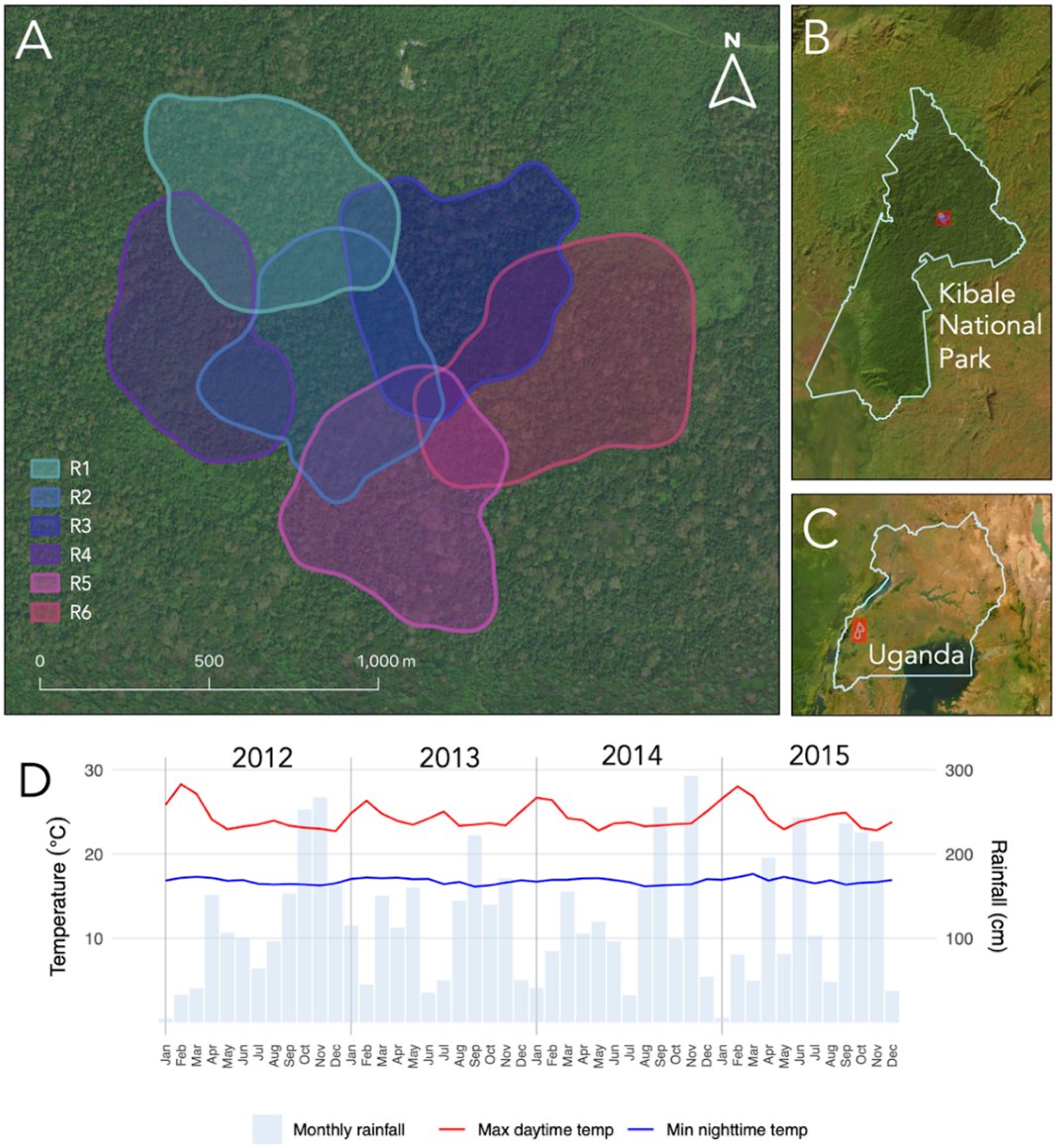

Figure S3.1. Study site and weather. Home ranges of six red-tailed monkey groups (**A**) at the Ngogo Research Station in Kibale National Park (**B**), Uganda (**C**), with inset maps in red. Rainfall and minimum and maximum temperatures are measured daily at Ngogo Research Station (**D**). The light blue bars represent the monthly sum of rainfall in cm, the red and blue lines represent monthly mean maximum daytime and minimum nighttime temperatures in °C. The satellite imagery basemap is produced by ArcGIS Online from sources: Esri, Maxar, Earthstar Geographics, and the GIS User Community (Esri, 2009).

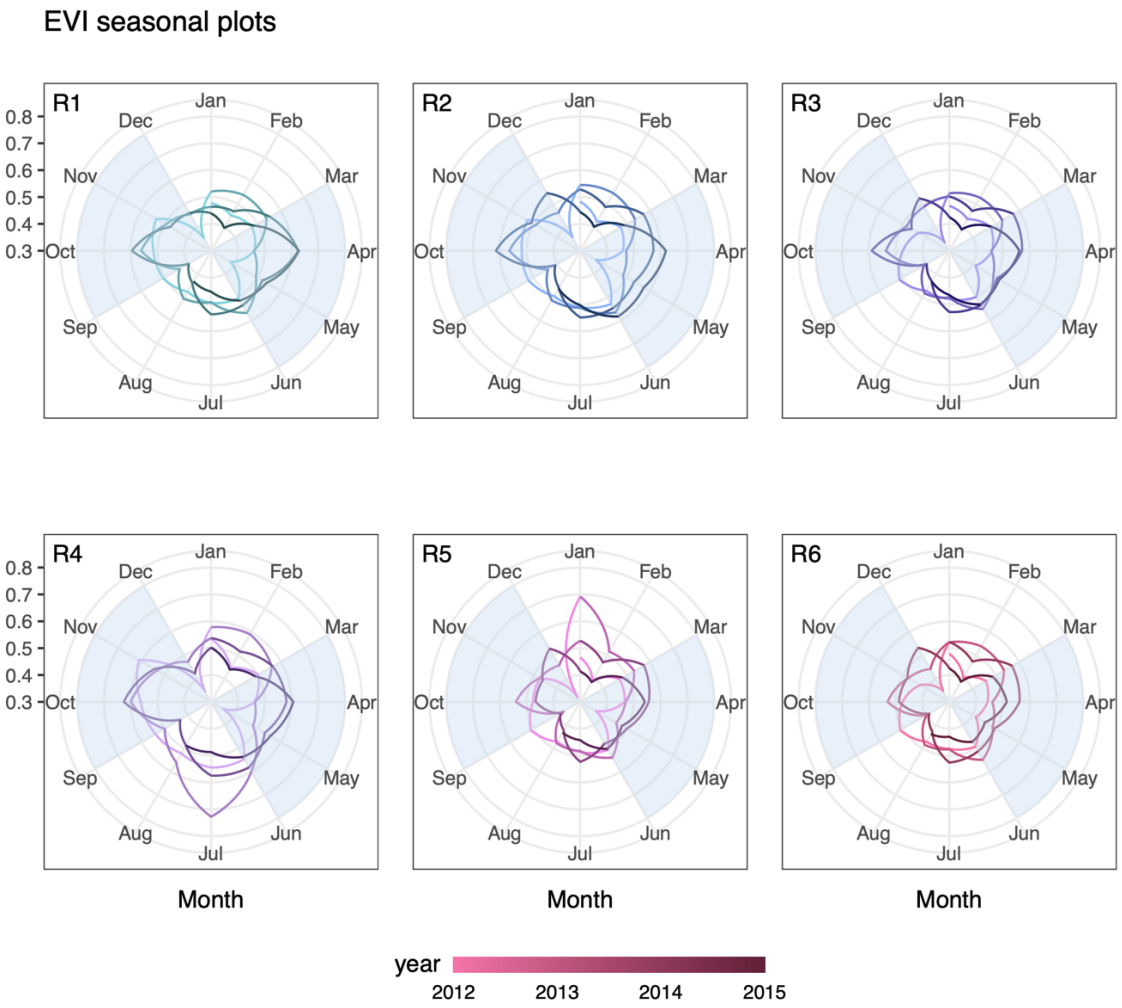

Figure S3.2. EVI Seasonal Plots. Seasonal variation in Enhanced Vegetation Index (EVI) across six monkey home ranges at the Ngogo Research Station, Kibale National Park, from 2012 to 2015. Each line represents the annual EVI trend for one of the six monitored monkey home ranges (groups R1-R6), with line color intensity increasing with later years (darker lines indicate more recent years). Light blue shaded regions illustrate the two annual rainy seasons, running roughly March-May, and September-November every year.

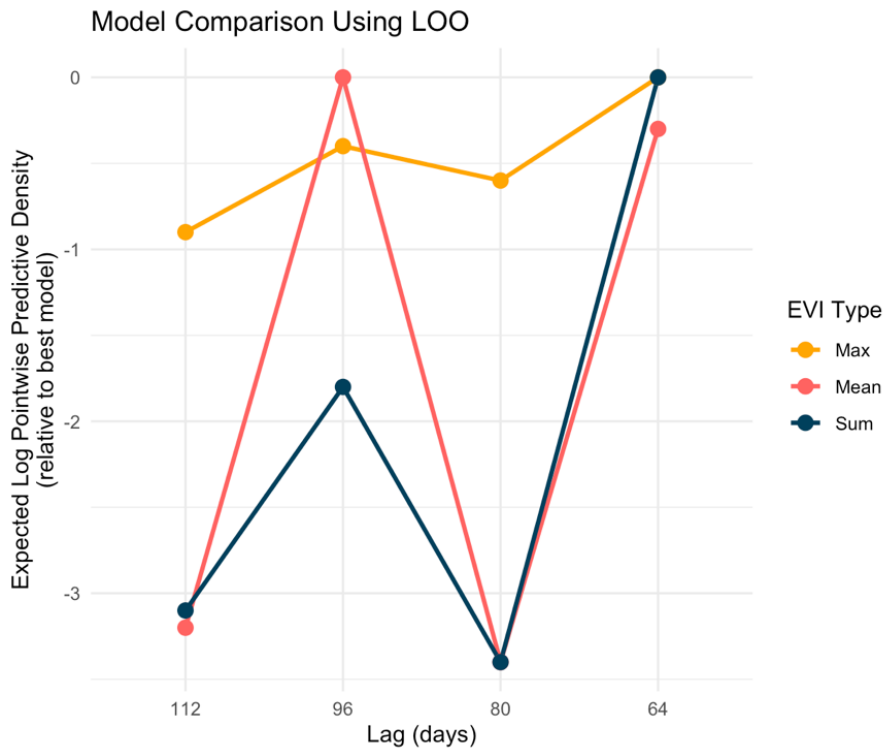

Figure S3.3. Model Comparison Using Leave-One-Out Cross-Validation (LOO) for Different Lags and EVI Metrics. This figure shows the model comparison using LOO for three EVI metrics (mean, max, and weighted sum) at lags of 64, 80, 96, and 112 days prior to UCP measurements. The elpd_diff (expected log predictive density difference) values are presented, with lower values indicating worse predictive performance compared to the best-performing model (elpd_diff = 0). Mean EVI at a 96-day lag shows the strongest predictive performance, followed by the 64-day lag, while other models demonstrate weaker predictive power.

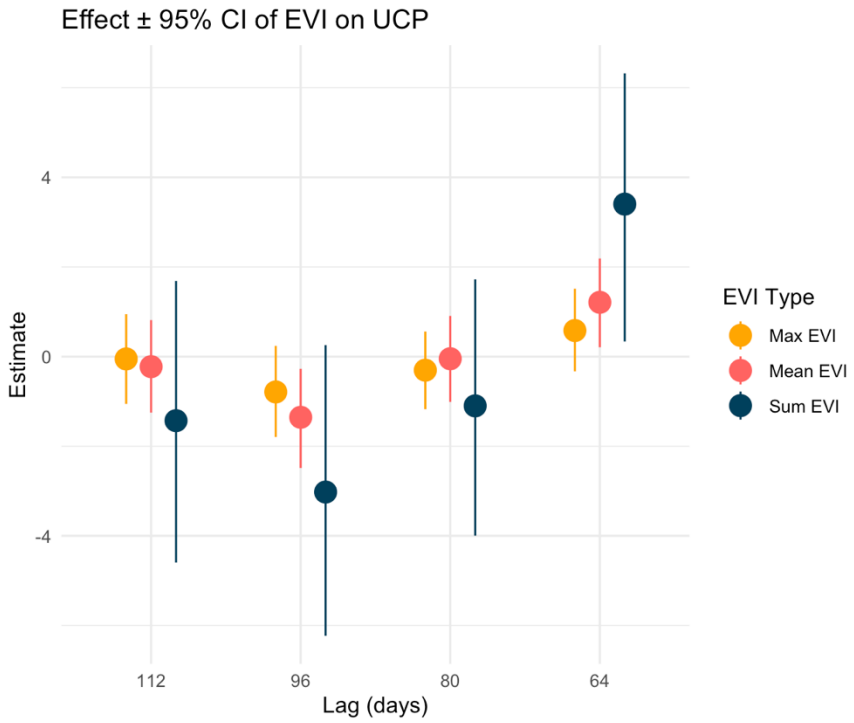

Figure S3.4. Effect Sizes and Confidence Intervals for the Impact of EVI on UCP at Different Lags. This figure displays the estimated effect sizes of mean, max, and weighted sum EVI on UCP, along with their 95% credible intervals, across four lag periods (*Period –4*, 64 days; *Period –5*, 80; *Period –6*, 96; and *Period –7*, 112). Positive estimates suggest a positive relationship between EVI and UCP, while negative estimates suggest a negative relationship. The figure highlights the consistent predictive power of mean EVI at a 96-day lag, with other metrics showing varying levels of influence.

6.3 SUPPLEMENTAL INFORMATION, CHAPTER IV

6.3.1 Figures

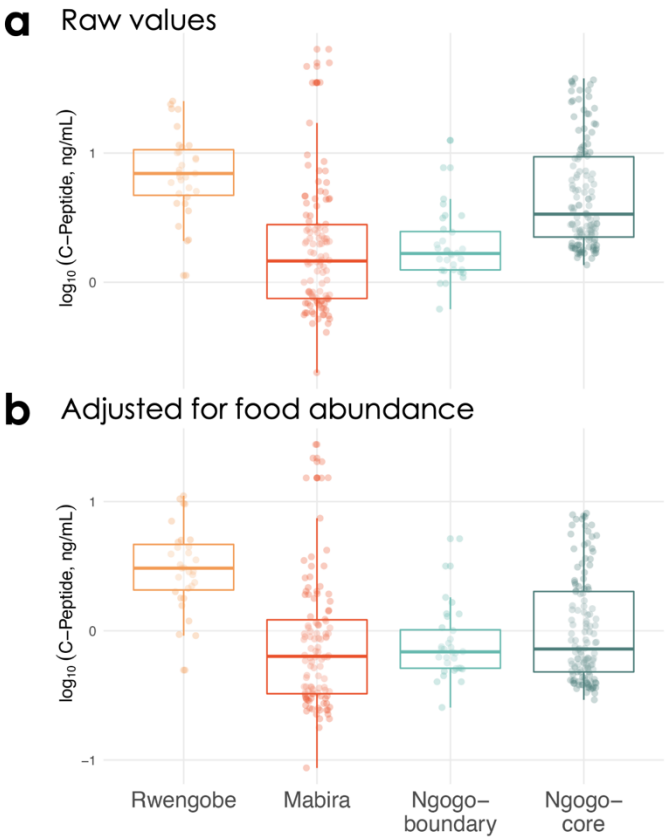

Figure S4.1. Preliminary results from the 2019 pilot study. Red-tailed monkey energy balance from groups at the four study sites in Uganda, each with a different number of competing species (from left to right, 0-3). Jittered points and boxplots are urinary C-peptide values (adjusted by specific gravity). a) log-transformed C- peptide values. b) the residuals from a regression of C-peptide values against fruit availability scores; when controlling for fruit availability, groups of red-tails with competitors (Mabira, Ngogo boundary, Ngogo core) exhibit worse energetic condition compared to those living without competitors (Rwengobe) with similar residuals regardless of the number of competing species in the habitat, which supports H2.

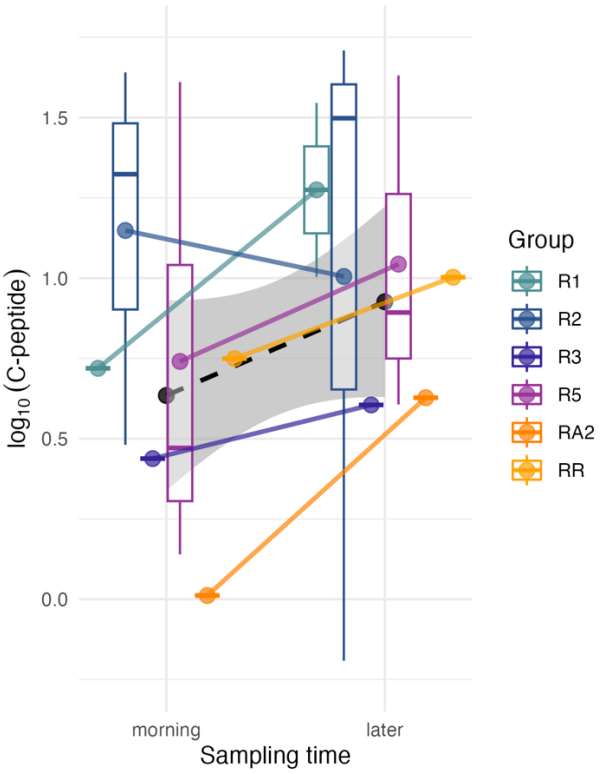

Figure S4.2. Mean urinary C-peptide (UCP) by time of day. The difference between first morning voids (fasting values, which represent overall energy stores) and urine samples collected later in the day (post-feeding values, which represent short-term surges in response to feeding). Boxplots represent all log-transformed UCP values for each group and observation period, and colored lines and points represent the log-transformed mean per group. The dashed black line and ribbon represent the global regression ($p < 0.05$) and its 95% confidence interval for all groups. Only individuals with both morning and afternoon values from the same day were included (N = 108 individuals total; R1: 11 individuals; R2: 35; R3: 2; R5: 12; RA2: 42; RR: 6).

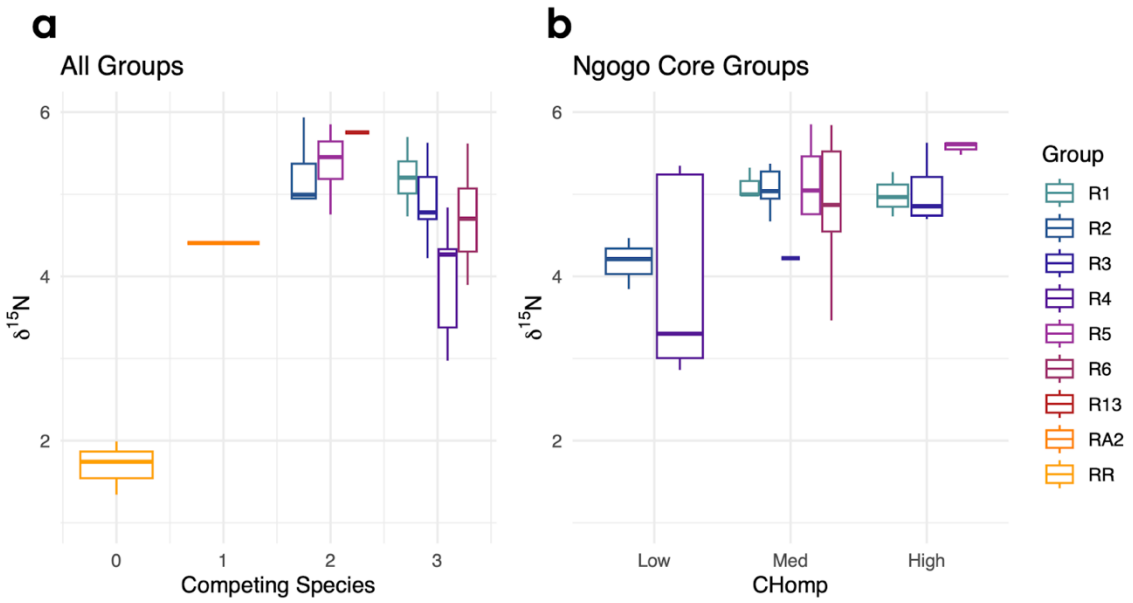

Figure S4.3. Nitrogen Isotope Values Across a Gradient of Competition. a) $\delta^{15}N$ values per group per observation period with respect to the number of competing species in their habitat (Table 4.1) for all groups in the study. **b)** $\delta^{15}N$ values from Ngogo Core groups with respect to the chimpanzee competition index, CHomp. CHomp was binned into low (index values < median - 1SD), medium (values in the range of the median ± 1SD), and high (values > median + 1SD). Boxplots display the median and interquartile range of values.

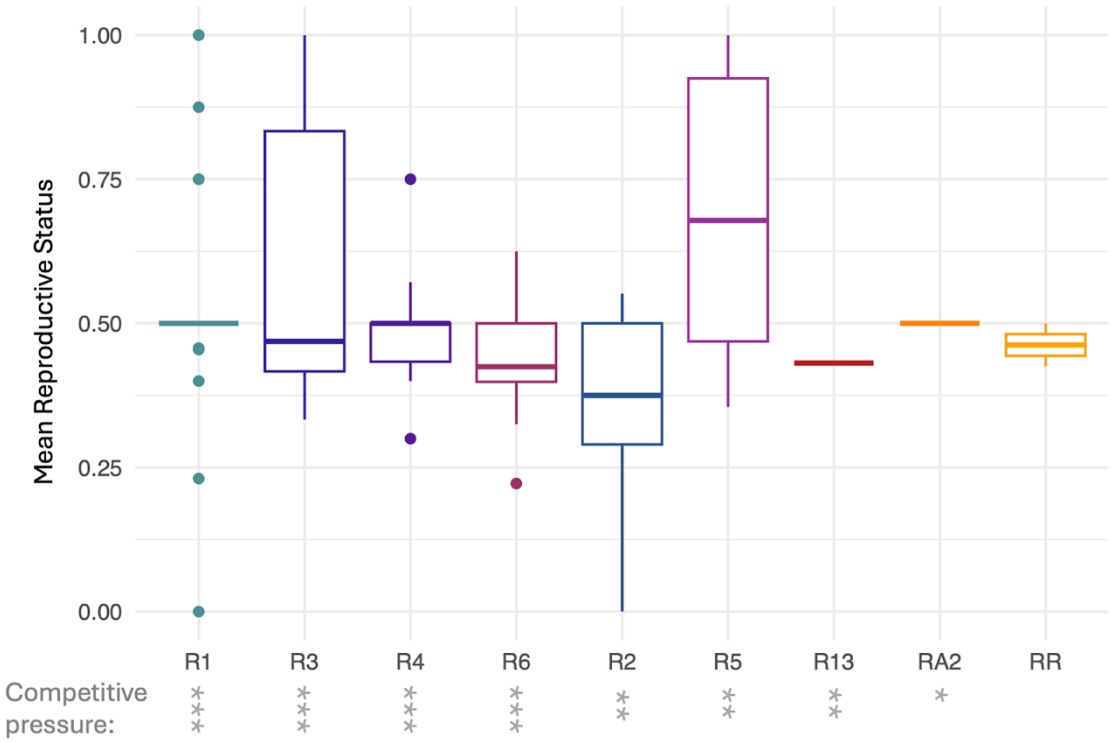

Figure S4.4. Reproductive Productivity Across Groups. Boxplots representing the variation in the mean reproductive value assigned to each group for each observation period. The status of each female in each sampling period is determined by estradiol levels (cycling and gestational phases of reproduction) and observations of nursing status of dependent young (lactational amenorrhea). Each female is assigned a monthly score (0=cycling; 0=non-cycling; 1=pregnant). The average score per group and season is the index of group-wide reproductive activity and scales from 0 (no reproductive effort by anyone) to 1 (all females pregnant). Asterisks denote the relative degree of competitive pressure that each group experiences (none, * = low; ** = med; *** = high; Table 4.1).

6.3.2 Tables

Table S4.1. Age-sex Class Differences in Biomarker Values. Results from a series of ANOVA tests followed by post-hoc Welch's t-tests to identify pair-wise differences for each biomarker between age-sex classes (AF = adult female; AM = adult male; SF = subadult females; SM = subadult male) of red-tailed monkeys. SF were excluded from $\delta^{15}N$ tests because no isotope data exists for this age-sex class.

Biomarker	Classes	N_1	N_2	t	df	p-value	adj. p-value	
CR:SG	AF - AM	1146	122	-2.53	152	**0.01**	0.06	ns
	AF - SF	1146	20	-2.94	19.7	**0.01**	**0.05**	*
	AF - SM	1146	54	-1.27	59.9	0.21	0.42	ns
	AM - SF	122	20	-1.81	24.8	0.08	0.25	ns
	AM - SM	122	54	0.50	109	0.62	0.62	ns
	SF - SM	20	54	2.00	30.4	0.05	0.22	ns
UCP	AF - AM	1676	182	-0.13	211	0.90	1.00	ns
	AF - SF	1676	43	6.65	82.5	**<0.001**	**<0.001**	****
	AF - SM	1676	114	0.53	128	0.60	1.00	ns
	AM - SF	182	43	3.31	222	**0.001**	**0.01**	**
	AM - SM	182	114	0.50	265	0.62	1.00	ns
	SF - SM	43	114	-2.44	143	0.02	0.06	ns
T3	AF - AM	235	12	0.86	11.8	0.41	1.00	ns
	AF - SF	235	8	-1.45	7.47	0.19	0.94	ns
	AF - SM	235	16	-0.78	15.5	0.45	1.00	ns
	AM - SF	12	8	-1.67	16.7	0.11	0.68	ns
	AM - SM	12	16	-1.14	24.8	0.26	1.00	ns
	SF - SM	8	16	0.21	22	0.84	1.00	ns
Ketones	AF - AM	82	8	1.35	85.5	0.18	0.58	ns
	AF - SF	82	3	1.89	83	0.06	0.34	ns
	AF - SM	82	9	0.64	53.6	0.53	0.86	ns
	AM - SF	8	3	2.25	7.68	0.06	0.34	ns
	AM - SM	8	9	-0.83	9.15	0.43	0.86	ns
	SF - SM	3	9	-1.60	8.7	0.15	0.58	ns
$\delta^{15}N$	AF - AM	225	12	-0.36	13.6	0.72	0.72	ns
	AF - SM	225	16	-1.73	17.9	0.10	0.30	ns
	AM - SM	12	16	-1.08	25.9	0.29	0.58	ns