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# An Empirical and Theoretical Comparison of the Socio-ecological Behaviors of Captive Chimpanzees (*Pan troglodytes*), Bonobos (*Pan paniscus*), and Western Lowland Gorillas (*Gorilla gorilla*): Social Tolerance and Behavioral Responses to Changes in Food Quality and Distribution

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An Empirical and Theoretical Comparison of the Socio-Ecological Behaviors of Captive Chimpanzees (*Pan troglodytes*), Bonobos (*Pan paniscus*), and Western Lowland Gorillas (*Gorilla gorilla*): Social Tolerance and Behavioral Responses to Changes in Food Quality and Distribution

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## Abstract

The three African Great Apes; gorillas, chimpanzees, and bonobos; each have species specific behavioral traits that have been hypothesized as being intricately linked to the feeding ecology of each species. However, though each species is unique in some aspect of their socio-ecological behavior, there are some parallels that can be drawn, such as the utilization of THV and cohesive groups in gorillas and bonobos. More specifically, relationships between the use of THV as a food source and maintenance of group cohesion in bonobos and gorillas have been contrasted with high degrees of frugivory and general aggression in chimpanzees. These parallels between bonobos and gorillas become more interesting when their geographical distribution is considered. Bonobos live allopatrically, separated from chimpanzees and gorillas by the Congo River, whereas chimpanzees and gorillas are sympatric in most of their range. As a result of this, it is thought that potential for ecological competition between gorillas and chimpanzees may have led to a divergence in the socio-ecological strategies of chimpanzees and bonobos. Direct behavioral comparisons of all three species are remarkably scarce in the literature, but these types of comparisons are necessary to determine the behavioral characteristics that may have been present in the last common ancestor of the *Gorilla/Pan* lineages. Therefore, we sought to provide an empirical comparison of the social behaviors of captive chimpanzees, bonobos, and gorillas as well as a theoretical comparison in changing ecological conditions in order investigate similarities and differences between the three African Great Apes in terms of their socio-ecological behaviors. We hypothesized that gorillas and bonobos would both be more likely than chimpanzees to tolerate the presence of conspecifics in close proximity, particularly when the potential for intra-species competition is high (e.g. when feeding). We also hypothesized that theoretical analyses of the evolutionarily stable strategies (ESS's) of aggressive (chimpanzee-like) and affiliative (gorilla and bonobo-like) individuals in changing quality and patchiness of food sources would reveal peaceful, or non-aggressive traits (e.g. those hypothesized to be gorilla or bonobo-like) when food is low quality and abundant, but aggressive

(or chimpanzee-like) traits when food is high quality and scarce. The results of our behavioral analysis indicated that bonobos were in fact the most tolerant of the three African Great Apes (as evidenced by time spent in close proximity to conspecifics) in feeding/foraging contexts, but that gorillas were the least tolerant in these contexts. In resting contexts, we found that chimpanzees were most tolerant of the three species and that gorillas were, again, the least tolerant in this context. Moreover, we did not find any significant similarities between bonobos and gorillas in terms of social tolerance in feeding/foraging, resting, or other contexts when behavioral analyses were run. In fact, in all contexts, gorillas were more the least likely of the three species to be in close proximity to conspecifics, and in feeding/foraging contexts specifically, bonobos and gorillas were significantly different in the amount of time they were spending alone ( $p < 0.05$ ). When analyzing just females of each species, we found trends similar to those seen when both sexes were analyzed. When theoretically manipulating food quality and dispersal, we found that, in environments with high quality but patchy food sources, it was evolutionarily stable for two individuals to be aggressive. However, in conditions that mirrored a THV dominated environment (those with low quality, but abundant food sources) we found that peaceful behaviors emerged as evolutionarily stable strategies.

## 1- Introduction and Background

In the majority of their range, central chimpanzees (*Pan troglodytes troglodytes*) and western lowland gorillas (*Gorilla gorilla gorilla*) experience high degrees of habitat overlap and often share the same or similar range areas and resources (Stanford and Nkurunungi, 2003; Head *et. al*, 2011). Dietary overlap, specifically in plant food, is high among the two species and habitat use patterns seem to be similar in areas where the two species live sympatrically (Kuroda *et. al*, 1996). In addition, western lowland gorillas (WLG's), the gorilla subspecies with the most significant habitat overlap with chimpanzees, tend to be more frugivorous than other gorilla subspecies' and therefore have the most potential for ecological competition with chimpanzees (Watts, 1996). Moreover, western lowland gorilla groups have even been observed to fission-fusion to some degree, though less pronounced than chimpanzees and bonobos. This behavior contrasts highly with that of montane gorillas, which feed almost exclusively on THV, and reflects the frugivorous nature of WLG's, suggesting even higher potential for competition with chimpanzees (Watts, 1996).

In contrast, bonobos (*Pan paniscus*) live free of habitat overlap from either of the two other species, yet occupy and utilize habitats that are ecologically similar to those occupied by chimpanzees and gorillas. In fact, many of these areas are at identical latitudes with separation occurring only by way of the Congo River, suggesting that ecological factors like food patch size and variation likely do not have enough of an impact alone to account for species differences among the three African apes (Wrangham *et. al*, 1996; Yamagiwa, 1999; Yamakoshi, 2004). It has therefore been hypothesized that the geographical isolation of bonobos as opposed to the geographical overlap of chimpanzees and gorillas in much of their range, may have led to many of the species specific traits observed in chimpanzees, bonobos, and gorillas. The effects of this can be seen in similarities and differences in habitat use, and sociality among conspecifics (Tutin *et. al*, 1991; Malenky *et. al*, 1994; Wrangham, 1986; Yamakoshi, 2004). Among these similarities and differences are variations in social structure, such as large versus

small group sizes, as well as resource exploitation. Bonobos and gorillas seem to be generally more gregarious with stronger female-female bonds and larger average group sizes, whereas chimpanzees tend to have slightly smaller groups, becoming even smaller when foraging (White and Chapman, 1994; Stanford and Nkurunungi, 2003; Sousa and Casanova, 2006). Chimpanzees also differ in that males are the dominant sex and male-male bonds are more prevalent than those between females (Wrangham *et. al*, 1996).

These differences in socio-ecological behavior, especially in the strength of bonds between females of the three species, are thought to be caused in large part by the foraging profiles and habitat use patterns of the three apes. The characteristics of these differences form the basis for the THV hypothesis, suggesting that sympatric chimpanzees may compete with gorillas for access to THV while bonobos are free of such competition (Wrangham, 1986). This distinction is thought to be a major cause of the social differences, such as group within group aggression and prevalence of female-female bonds, observed between chimpanzees and bonobos and may also account for some of the social behaviors seen in WLGs (Wrangham, 1986; Yamakoshi, 2004). However, doubts have been cast on the THV hypothesis, specifically as it relates to social relationships of the African Great Apes. These arguments are based in the lack of empirical support that has historically been provided for the hypothesis. The relationships between social characteristics and ecological profiles have therefore been debated heavily, with some researchers claiming that there is not enough evidence that THV alone has led to the social differences in the three African Ape species (Yamakoshi, 2004). Despite this claim however, direct comparisons of all three ape species in similar habitats using identical methods are nonexistent (but see Wrangham, 1986 for an overview of their ecology). Difficulties in collecting these kinds of data from wild apes have historically come from issues maintaining consistent visibility of focal individuals, and lack of control of ecological variables, thus leading to relatively inconclusive results (White and Wrangham, 1988; Yamakoshi, 2004). As such, this study aimed to address the basic similarities and differences in

social behavior between the three species in relation to their documented socio-ecological characteristics.

## **2- Social and Ecological Comparisons**

### **A) Ecology**

Important differences exist in the foraging strategies of all three African Great Ape species. Most notable among them is the tendency for gorillas and bonobos to use THV as a fall back food in times of fruit scarcity. This is often contrasted with the maintenance of relatively higher levels of year round ripe fruit foraging and consumption by chimpanzees regardless of its seasonal abundance (White, 1998; White and Wrangham, 1988; White and Chapman, 1994). These differences are reflected in species specific characteristics such as home and day range sizes, occupancy time spent at each food patch, seasonal shifts in food consumption related to relative food abundance, and in the diversity of foods eaten (White, 1998; Tutin, 1996). For example, while all three of these species are considered ripe fruit specialists, both gorillas and bonobos have a much broader range of staple fruits in their diet as well as high rates of consumption of pith, leaves and other THV compared to chimpanzees.

In respect to ranging patterns, western lowland gorilla home and day range sizes tend to be larger than other gorilla subspecies as a result of a greater reliance on fruit. However, these ranges still remain small, relative to chimpanzees with which they are sympatric, because of their ability to utilize more localized THV sources when fruit is scarce (Tutin, 1996). Chimpanzees, on the other hand, seem to be the only one of the three African ape species to extend their home range, rather than dietary breadth, in response to fruit scarcity in order to maintain a constant uptake of specific species ripe fruits (White, 1998; White and Wrangham, 1988). Contrastingly, both gorillas and bonobos tend to utilize a much larger variety of fruits when it is in season compared to chimpanzees (Malenky *et al*, 1994). Both also utilize THV at a constant level regardless of the relative abundance of fruit, suggesting a more



opportunistic fruit foraging behavior among them when compared to chimpanzees (Head, *et. al*, 2011; Yamagiwa *et. al*, 1996). Seasonal shifts in food consumption and a decrease of range area seem to be more pronounced in bonobos and gorillas while shifting to a larger range seems to be more common in chimpanzees (Yamagiwa, 1999). In fact, at some field sites, the Ndoki reserve in the Democratic Republic of Congo specifically, bonobos seem to parallel gorillas in many aspects of their feeding ecology including food preference and habitat exploitation, though direct comparisons between bonobos and gorillas have not been made (Malenky *et. al*, 1994). Reliance on vegetative food in gorillas and bonobos when fruit is scarce has consequently been cited as a causal factor leading to many of the observed social strategies in the apes. For example, these things have been found to play an important role in maintenance of female bonds and relatively large foraging groups in bonobos and gorillas, both of which are commonly contrasted with that of chimpanzees (Yamakoshi, 2004; Malenky and Stiles, 1991). See Table 1 for summarized comparisons of ecological characteristics.

#### B) Sociality

Similarities and differences among the three African Great Apes in the way the respective habitats of each species are exploited are thought to be inextricably linked to the social relationships between conspecifics and group structure of each species.

Chimpanzees are male dominated and tend to show male-male bonding around food sites, have weak alliances between females within a group, and form flexible fission-fusion groups with a highly promiscuous mating system (White, 1996; Wrangham *et. al*, 1996; Yamagiwa, 1999; Malenky *et. al*, 1994; Yamakoshi, 2004; Sakura, 1994). As a result of feeding competition and weak female bonding, chimpanzee groups are often forced to fragment when fruit is scarce, forming small foraging groups that are often highly aggressive (Stanford and Nkurunungi, 2003; White and Wrangham, 1988). These behaviors contrast highly with the social strategies of gorillas and many of them differ from those of

bonobos as well. Gorillas tend to have a lower level of within group feeding competition and therefore live in stable, cohesive groups where the use of THV presumably plays a critical role in competition regulation (Fossey and Harcourt, 1977; Tutin *et. al*, 1991; Head *et. al*, 2011). In fact, it has been suggested that the ability of gorillas, and bonobos, to utilize THV as fall back food may be one of the most important factors facilitating their relatively cohesive social groups (Tutin *et. al*, 1991; Malenky *et. al*, 1994; Wrangham *et. al*, 1996).

However, as mentioned above, there are doubts related to this claim, many of which stem from the lack of comparative data that exist on bonobos and gorillas. It seems that, overall, the link between THV presence and the gregariousness of folivore groups is sound in theory, however, few studies have provided sufficient data to claim that THV is the only factor leading to cohesive groups (Yamakoshi, 2004). Also unlike chimpanzees, gorillas seem to show higher levels of aggression to protect females as a resource rather than food as a resource. As a result of this, and because gorillas use THV as a fall back resource, gregarious relationships between females are not as costly as in chimpanzees and cohesive groups can be formed (Yamagiwa, 1999). Group foraging in gorillas is also facilitated by this relationship, and female-female aggression tends to be low in foraging scenarios. This relative lack of aggression often leads to multiple gorillas feeding and foraging in close proximity to conspecifics within a food patch (Watts, 1996; Yamagiwa, 1999; Head *et. al*, 2011; Hirsch, 2007; Malenky *et. al*, 1994). In fact, some studies have found that gorillas always forage in the company of a conspecific (Tutin *et. al*, 1991). This same study, however, does not explicitly define what is meant by the term “company”, and it is therefore unclear how dispersed individuals are while foraging, are exactly what is meant by tolerance or group cohesion. Similar to gorillas, bonobos maintain closer female-female bonds compared to chimpanzees, specifically while foraging when females are far more likely to be in close contact with one another than with a male (White and Chapman, 1994). As in gorillas, large parties in bonobos are thought to be facilitated by relatively low levels of feeding competition compared to chimpanzees and

group foraging strategies are often modified to maintain cohesive groups when fruit is scarce. Tolerance of conspecifics, as evidenced by close proximity during feeding, also seems to parallel that of gorillas as do bonobo female-female relationships (Furuichi et. al, 2001; Yamakoshi, 2004; Yamagiwa, 1999; White, 1996). Some of these studies, again, are unclear on how proximity is defined. Though many of the social traits of bonobos are comparable to those of gorillas, there are some that are more characteristic of chimpanzees. Bonobos still show group fission and fusion to some extent; however bonobo groups tend to change less frequently than chimpanzees and fission-fusion groups are much more likely to be age-sex diverse (Watts et. al, 2012; White and Wrangham, 1988). Bonobos also often remain clumped into groups within one or a few fruit trees when fruit is abundant while chimpanzees disperse evenly among trees. This is thought to be a major way in which the two ape species regulate how close conspecifics are when feeding on high quality foods (White, 1996; Hohmann and Fruth, 1994). See Table 2 for a summarized comparison of the social characteristics of the three species.

These social differences are thought to be influenced by differences in the use of THV as a supplemental food source in each species (Wrangham et. al, 1996). Additionally, it has been suggested that the absence of gorillas in bonobo habitats may have allowed for increased reliance on THV and therefore facilitated their social relationships (Malenky and Wrangham, 1994; Yamakoshi, 2004). Similarly, the sympatry of chimpanzees and gorillas in some of their range has been hypothesized as a causal factor for many of their social characteristics. As a result of this, it is important to understand the effects of sympatry on the socio-ecological behaviors of the species. As such, a direct comparison of the social behavior of chimpanzees, bonobos and gorillas using the same methods in populations living in controlled habitats is useful to help clarify basal similarities and differences in the behavior of each species.

### C) The Significance of Sympatry

Socio-ecological characteristics of the three species become particularly important when the sympatry of chimpanzees and gorillas is considered. Range overlap in these two species has occurred relatively recently over the course of their evolutionary lineages. Extensive overlap of these two species in much of their range suggests increased potential for competition when preferred food is scarce, and may have led to increased speciation in gorillas and chimpanzees. As chimpanzees and bonobos are genetically more related to each other than either is to humans or gorillas, there is the possibility of specialization in common chimpanzees after an initial split between the *Gorilla/Pan* lineages. Molecular data using mitochondrial DNA sequencing have dated the divergence of the *Gorilla/Pan* lines at somewhere between 7 and 10 million years ago (MYA) (Sibley and Aulquist, 1984; Patterson *et.al*, 2006; and Zihlman *et. al*, 1978). Similarly, these same data have estimated that the *Pan* lineage diverged from *Homo* around 6-8 MYA and that of chimpanzees and bonobos subsequently diverged from each other somewhere in the range of 1-2 MYA (Sibley and Aulquist, 1984), although these dates are still being verified. The current timeline, however, suggests that bonobos are likely the best model from which to build assumptions about the common ancestor to leading to all African Great Apes. Bonobos have been documented as being more generalized in their behavior and foraging strategies than chimpanzees or gorillas. As such, an overlap in the ranges of the latter two species may have provided pressure for specializations in their socio-ecology leading to the development of what we now know as *Pan troglodytes* and *Gorilla* (Zihlman *et. al*, 1978). The divergence of the *Pan* line from the *Gorilla* line correlates well with the Tertiary and Quaternary Periods of the Miocene Epoch, occurring approximately 5-10 million years ago. The ecological changes associated with these periods are thought to have led to niche convergence of the African Apes, and may have provided pressure for the development of different foraging strategies, leading to different social characteristics (Yamagiwa *et. al*, 1996). Therefore, it is probable that, at some point during the major environmental changes of this period, the

*Gorilla/Pan* lineages were split by the Congo River, forming the habitat of *Pan paniscus* without overlap of *Gorilla* or *Pan troglodytes*. This separation likely allowed bonobos to revert back to traits characteristic of a common ancestor of all three species (Zihlman *et. al*, 1978) while chimpanzees and gorillas overlapping in areas north of the Congo River had to continue to develop specialized traits to avoid competitive exclusion.

Instances of aggressive displacement during co-feeding on food patches between chimpanzees and gorillas in areas where the two are sympatric have been observed in the Democratic Republic of Congo at the Ndoki Reserve, the Republic of Congo at the Goulougo Triangle, and in Uganda at the Bwindi Impenetrable Forest (Yamagiwa *et. al*, 2012). Most interspecific encounters to this point seem to show mutual avoidance rather than aggression, although some studies do suggest scramble competition between chimpanzees and gorillas (Yamakoshi, 2004). It is clear, however, that the mere potential for competition in overlapping populations does have some effect on diet use and ranging patterns, causing chimpanzees to range further and gorillas to expand their diets (Yamagiwa *et. al*, 1996). It is therefore important to understand if, and to what extent, the social and ecological characteristics of each species have provided an evolutionary pressure for niche divergence, especially when fruit is scarce. As a result of the importance of THV to the diet of gorillas, consistent foraging on this food source has been suggested as a major pressure reducing the ability for sympatric chimpanzees to utilize it in the same way. Therefore, sympatry seems to have promoted different fall-back foraging and social strategies in chimpanzees and gorillas as a way to regulate interspecies competition (Yamagiwa *et. al*, 2012; Wrangham *et. al*, 1996). Bonobos, however, seem to have social, communicative, and foraging strategies that are at somewhat of an intermediate point between the extremes of gorillas and chimpanzees. That is, communicative strategies in bonobos are more similar to chimpanzees than to gorillas (Hohmann and Fruth, 1994; Pollick and De Waal, 2007), while social strategies and foraging profiles parallel gorillas more than chimpanzees (Wrangham, 1986; Tutin *et. al*, 1991; Yamakoshi, 2004).

It has therefore also been hypothesized that the absence of gorillas and chimpanzees in bonobo habitats may have allowed for them to retain the use of THV and allowed for the maintenance of certain aspects of sociality, foraging, and communication that parallel characteristics seen in the other two apes. As such, it is possible that a combination of these traits may reflect the characteristics of the common ancestor to all three species (Malenky *et. al*, 1994; Tutin *et. al*, 1991; Head *et. al*, 2011). Socio-ecological differences between chimpanzees and bonobos may therefore be a result of the availability of THV (through the presence or absence of gorillas) in their respective habitats (Wrangham *et. al*, 1996; Wrangham, 1986).

For sympatric species as phylogenetically close as chimpanzees and gorillas, mechanisms leading to niche differentiation must exist in order to avoid displacement and possible competitive exclusion of the least fit species (Tutin, *et. al*, 1991). Impacts of ecology and the presence of morphologically similar competitors on behavioral traits is possible to assess through a direct comparison of sympatric species. Therefore, it is beneficial to directly compare the three African ape species in regards to fundamental characteristics of their socio-ecology (Tutin, *et. al*, 1991; Yamakoshi, 2004). This may help to assess the direct impact of the presence of gorillas on the formation of social behaviors and the divergence of chimpanzees and bonobos (Yamakoshi, 2004). Unfortunately, wild studies directly comparing the three species are difficult to carry out at best, and data on western lowland gorillas have been particularly difficult to collect and are therefore inconclusive (Yamakoshi, 2004; Yamagiwa, 1999). However, there are strengths in captive studies for assessing the ancestral traits of these species because comparing all three species in a controlled environment may elucidate species-typical traits that were present before the divergence of the two genera.

#### D) The Importance of Captive Studies

Data on all three African ape species in the wild have been collected with an emphasis on behavioral ecology and foraging strategies in times of fruit scarcity (Head et. al, 2011; Malenky and Wrangham, 1994; Malenky et. al, 1994). However, relatively few field studies exist that directly compare the socio-ecology of all three species using the same methods (but see Wrangham, 1986 for an assessment of the impact of THV on each species), and even fewer captive studies exist with that aim. The captive data that do exist tend to place emphasis on defining dominance hierarchies or aggressive behavior in different feeding conditions (Scott and Lockard, 2006 in western lowland gorillas). Though some studies comparing great ape social behavior exist, the literature is still relatively sparse in regards to those that provide a direct comparison of the three African great apes. The central issue for understanding the relationship between chimpanzees and gorillas seems to be how they utilize fruit resources (Kuroda *et. al*, 1996). However, sufficient data on foraging profiles of all three African apes in terms of the way that they each exploit fruit, especially in areas where gorillas and chimpanzees are sympatric, is lacking due to difficulties with consistent access to populations.

Though issues with potential habituation to feeding schedules and diets likely influence aspects of captive ape behavior, many of the issues with variability of environmental conditions that are characteristic of wild studies can be controlled for in captive studies. Food items, dispersal, group size, and group composition, among other things, are often kept very similar for all three African Great Apes across zoos. As data from similar habitats are essential for comparing the socio-ecology of the three African Great Ape species (Malenky *et. al*, 1994), removing confounding ecological factors and controlling for the above variables can only be accomplished by using captive populations. Additionally, western lowland gorillas are currently the only gorilla species housed in captivity in the United States, and are also the species with the most significant overlap in habitat and foraging profile with chimpanzees, making them ideal candidates for a socio-ecological comparison. As such, the data

presented here provide a simple, but novel, comparison of the three African Great apes in terms of their social behavior. Comparisons of intraspecific traits of each of the three species can be used to imply the effects of interspecies interactions that have occurred over the evolutionary history of the African Great apes. This is especially possible when confounding variables present in wild populations are controlled for by studying captive populations. In this way, species-typical similarities and differences should present themselves when the exact same methods are used. Habituation to the possibility of competition as it relates to feeding is to be expected in captive populations. However, if differences do emerge it is probable that those differences are species specific if the same methods have been used and if conditions are kept the same for each population. To date, there have been no comparative studies of all three African Great apes in captivity, very few comparisons in the wild, and none using the same methods.

### **Behavioral Hypotheses**

Based on the characteristics of the feeding ecologies and socio-ecological strategies of chimpanzees, gorillas and bonobos described above, we aimed to address how the three African ape species compared to one another across multiple contexts in respect to their social tolerance. As relationships between the exploitation of food sources, social structures, and group cohesion have been suggested as similarities in gorillas and bonobos, we sought to provide a simple, but direct, comparison of the social characteristics of the three African great apes. Similarly, as chimpanzees seem to have somewhat extreme social, and less flexible ecological, characteristics compared to the other two apes, it was reasoned that similarities and differences would arise in basic socio-ecological characteristics when the same observational methods were used for each species. As such, the hypotheses for this study were as follows:



Due to parallels in the consumption of THV and in the foraging profiles, as well as similarities in group cohesion, strength of female-female bonds and general within-group gregariousness in gorillas and bonobos we hypothesized that:

- 1) *Gorillas and bonobos will be more likely than chimpanzees to tolerate conspecifics in close proximity across multiple contexts and will be more similar to each other than to chimpanzees in this regard.*

As a result of the aggressive nature, weak female bonds, and small foraging groups observed in chimpanzees, and the tendency to maintain ripe fruit as a staple of their diet in the wild, we hypothesized that:

- 2) *Chimpanzees will be less likely to be tolerant of conspecifics in close proximity, especially in feeding contexts, than both bonobos and gorillas.*

## **Methods**

In order to test the behavioral hypotheses listed above, a direct comparison of captive chimpanzees, gorillas, and bonobos housed at American Zoological Association (AZA) accredited zoos was carried out using identical behavioral ethograms and data collection methods for each species. Methods were kept purposefully simple to provide as direct a comparison as possible between the three species. Descriptions of study sites, group dynamics and group management for each species are as follows.

### Subjects and Study Sites

#### *Chimpanzees- North Carolina Zoological Society, Asheboro, North Carolina*

The chimpanzee enclosure at the North Carolina Zoo is approximately 45,000 square feet of outdoor space. Accessible to the chimpanzees are numerous large rocks, real and fake, as well as downed trees and large patches of grass. There is a large, fake tree, hollowed out on the bottom, in one corner of the enclosure that is commonly used as a climbing structure or as cover from the sun or rain, as well as patches of real trees protected by hot-wire. The enclosure also has a dry mote that surrounds the entire yard, approximately 6-8 feet deep, that the chimpanzees can access. Surrounding the

chimpanzee exhibit are two large visitor viewing areas with glass walls that the chimpanzees commonly sit near while grooming or interacting with visitors.

North Carolina's chimpanzee group consists of 17 total chimpanzees ranging from 1 year to approximately 46 years old. These animals are separated into two groups that occasionally have 1-2 females transferring between groups, males are never transferred, to simulate chimpanzee fission-fusion social structure. The groups therefore have 4 males and between 4-6 females (group 1) and 1 male and between 4-6 females (group 2) in them on any given day. In the first group one of the males is 1 year old and was therefore not included as a focal individual, and in group 2 one of the females is 2 years old and were not included as a focal individual as these were determined to be infants with the potential to still be dependent on their mothers. Therefore the number of focal individuals in each group on a given day ranged from 7-9 (3 males, 4-6 females; group 1) and 5-7 (1 male, 4-6 females; group 2). On any given day, one of the two groups of chimpanzees had access to the outdoor yard until 2:00, at which time this group was brought to the inside enclosure, food was spread in the yard, and the second group was given access to the yard until 2:00 PM the next day. The individuals that were transferred between groups did so on a random basis by being allowed the option to self-transfer and therefore had the potential to be in both groups on the same day.

At the North Carolina Zoo, whichever group of chimpanzees had access to the yard over night was typically brought inside for a short time in the morning while keepers spread food evenly throughout the enclosure. This group was then given access to the yard again and allowed to forage until approximately 2:00 PM. After this time, the first group would be brought in, food would be spread again, and the second group would be let out until 2:00 PM the next day. Food spread in the yard at the North Carolina Zoo consisted of primate chow (a low quality grain and protein source), leafy vegetables (lettuce, kale, spinach), sweet potatoes, carrots, green beans, and other vegetables. Occasionally, enrichment items (peanut butter spread on paper towel rolls, toys filled with yogurt, etc.) were thrown

from a feeding platform in the afternoon in addition to the normal food dispersal. Higher quality foods and those high in sugar, such as fruits, were typically saved until the group was brought inside and used for their evening diet. Individuals of the outside group of chimpanzees would also commonly forage on grass and other vegetation growing the yard.

*Gorillas- Zoo Atlanta, Atlanta, Georgia*

Zoo Atlanta's family group of western lowland gorillas is housed in a 17,850 square foot yard. Within this enclosure are multiple large piles of rocks as well as numerous trees protected by hot-wire. There is also a large, fake, hollow tree inside the enclosure that has 2 hammocks hanging from it and is commonly used by the gorillas as shade or a place to rest. Zoo Atlanta's gorillas also have access to a small ditch that runs alongside the visitor glass of one of the three viewing areas.

The family group of gorillas at Zoo Atlanta consists of 11 gorillas that range in age from just under 2 years old to 31 years old. Of the 11 gorillas in the family group, 9 of them were included as focal individuals for this study, two were under 2 years of age at the time of the study and were therefore determined to be infants with the potential to still be dependent on their mothers, and were not included as a focal individual. Along with the male silverback of the group, there was one other focal male (age 5) while all other focal individuals were females. All 11 gorillas were consistently in a group together during every day of data collection and there was never any transferring of individuals. However, part of the way through the study two of the focal females were removed from the group and moved to a different zoo before observations of them were completed.

At Zoo Atlanta, keepers spread primate chow, vegetables (mostly leafy greens as at NC Zoo), sweet potatoes, cucumbers, and other vegetables, evenly throughout the yard every morning. All 11 gorillas were then allowed access to the yard and were able to forage freely on their morning diet. At approximately 2:00 PM keepers would disperse "higher quality" foods (often sunflower seeds, peanuts,

or pieces of fruit) from a roof-top feeding area. This afternoon food would be thrown into large clump in one area of the yard, and some items would be thrown directly to the gorillas themselves. After the afternoon feeding, the gorillas were then able to forage freely again. The gorillas at Zoo Atlanta also commonly fed on dead leaves, grass, and other browse already in the yard.

*Bonobos- Jacksonville Zoo and Gardens, Jacksonville, Florida*

The bonobo enclosure at Jacksonville Zoo is approximately 6,940 square feet of outdoor space. Inside the enclosure, the bonobos have access to a three story climbing structure with multiple ropes and hammocks attached to it. There is also a small pool with a waterfall running into it when filled, though this pool was often empty and used for shade by the bonobos. Surrounding the bonobo yard is a moat running along the outside edge of the enclosure. The bonobos at the Jacksonville Zoo do not have any direct access to visitors via a glass viewing areas, but are instead viewed from visitor decks above the yard.

Jacksonville's bonobo group consists of 11 bonobos ranging in age from under 1-approximately 45 years old. There were 6 females and 4 males included as focal individuals for this study, as with the other two ape populations, the 5<sup>th</sup> male was excluded as a focal individual because he was under 2 years old and was determined to be dependent on his mother. Similar to the North Carolina Zoo, the bonobo groups at Jacksonville were switched on a daily basis to simulate their fission-fusion social structure. On any given day of data collection there were between 4-6 focal individuals in the yard (usually with 1-2 males and 3-5 females). On some days one group would have access to the yard for the entire day of data collection, while on others that group would be brought in at approximately 12:00 PM and the second group would be brought out for the rest of the day. Occasionally, there were 1 or 2 bonobos that were part of the morning and afternoon group on days that the groups were changed.

The feeding schedule at Jacksonville Zoo was similar to those of North Carolina and Zoo Atlanta. Keepers would spread the morning diet (consisting of vegetables, some fruits, and occasionally enrichment devices) evenly throughout the yard before the apes were allowed access. The morning group would then be allowed to forage freely on what had been spread in the yard. At approximately noon, the morning group would either be brought inside and more food would be spread for the afternoon group, or the morning group would be left outside and fruit and vegetables would be thrown into a large clump from a roof-feeding area.

#### *Behavioral Data Collection*

Data for each species were collected using identical methods at each zoo. Individual focal follows were randomly performed on a member of the focal group. Each individual in the group was assigned a number and the focal individual was then chosen using a random list organizer. If the individual to be followed happened to be chosen twice in immediate succession, then the next individual in the list was followed. Each focal follow consisted of 10 minutes of constant observation, during which a data point was taken for the focal individual precisely every 30 seconds starting at minute zero using instantaneous focal sampling. This resulted in a total of 21 data points per focal follow. During each focal follow, the focal individual's behavior was coded using the ethogram of behaviors provided (Table 3) and the proximity of the focal individual to any conspecific was also coded using the provided proximity ethogram (Table 4). Individuals could either be touching a conspecific(s); in physical contact; close to a conspecific(s); within 1.5 meters; or alone; greater than 1.5 meters from a conspecific(s). The use of 1.5 meters as a measurement of closeness was decided on based on the notion that individuals in this proximity would be hyper-tolerant of one another and were within slapping/pushing distance. If more than one conspecific was in proximity to the focal individual at the time of the data point, the proximity of each conspecific to the focal individual was coded for that data point. Proximities were pooled together into three categories; alone, close, and touching (Table 4). If the

focal individual was out of sight during a data point, that point was coded as “CBD” (cannot be determined) and if this continued for 6 straight data points that focal follow was discarded. Along with the behavior and proximity of the focal individual, instances of agonistic or affiliative behaviors were also noted along with the receiver of the behavior and the response of the receiver. At least 20 focal follows were performed on each individual of each species for a total of approximately 200 minutes of observation and about 420 behavioral data points per individual. For the two gorillas that were moved to a different zoo part way through the study, 17 focal follows were performed on each. Fourteen chimpanzees, ten bonobos, and nine gorillas were observed for this study.

### *Data Analysis*

Behavioral data were analyzed for both sexes as well as for just females of each species. Additionally, behavioral contexts from Table 3 were pooled into 3 categories; feeding/foraging, resting, and other. These three contexts were chosen as categories based on the assumption that the potential for competition and agonistic interactions would be highest in feeding/foraging contexts and likely the lowest in resting contexts when individuals presumably have the option to spend an extended period of time in close proximity to a conspecific or not without the potential cost of increased feeding competition. The percentage of time each individual spent alone in each of these three contexts was compared using a repeated measures ANOVA with species as the between subject factor. Group size was co-varied out for each species. Additionally, infants (individuals under 2 years old) were excluded from being counted as a social partner to a focal individual in the analysis. This was decided based on the assumption that individuals under 2 years old were still dependent on their mothers and likely did not present a competitive pressure for other individuals of the group. Therefore, if any focal individual was in close proximity to an infant of the group, for purposes of the analyses that focal individual was counted as “alone” unless they were also in proximity to a non-infant, in which case they were counted

as “not alone”. For each of the three pooled behavioral categories the percent of total time spent alone in each context was calculated using the following equation:

$$\frac{\textit{Total time spent alone in each context}}{\textit{Total number of data points in each context}}$$

Using SPSS boxplots of the total time alone in all contexts, three chimpanzees were identified as outliers, one male and two females, and were excluded from these analyses. Post hoc analyses of specific behaviors were run in Microsoft Excel to determine any differences between the three species in feeding/foraging, resting, or other categories specifically.

## **Results**

We collected 14,805 data points cumulatively across all three species, with 4,746 collected for bonobos, 6,405 data points for chimpanzees, and 3,645 data points for gorillas. In total, 118 hours of direct observation were analyzed for all three species combined.

We found a significant interaction between behavioral context and species ( $F(4,54)=5.068$ ;  $p=0.002$ ) when both sexes were included in the analysis, as well as a significant interaction when just females were analyzed ( $F(4,36)=3.46$ ;  $p=0.017$ ). Additionally, post hoc analyses using independent sample t-tests were run to compare the mean amount of time each individual of each species spent alone in feeding/foraging contexts. There was a significant difference between bonobos and gorillas in the mean percentage of time each species spent alone in feeding/foraging contexts ( $t(17)=2.132$ ,  $p<0.05$ ), but no difference when bonobos and chimpanzees were compared, or when chimpanzees and gorillas were compared. Gorillas were the most likely of the three apes to be alone across all categories (68.3% +/- 0.039; Figure 2), as well as in each individual category analyzed when both species and when just females were included (Figures 3 and 4). We also found that captive chimpanzees spend less time alone across all contexts than bonobos or gorillas (Figure 2; chimpanzees=45% +/- 0.036; bonobos=52%

+/- 0.059; gorillas=68% +/- 0.039). Bonobos, (regardless of sex) spend the least amount of time alone in feeding/foraging contexts compared to the other two species (68% +/- 0.048 both sexes, 66% +/- 0.055 just females; Figures 3 and 4). However, in resting contexts, chimpanzees spend much less time alone (38% both sexes, 46% just females; Figures 3 and 4). Finally, chimpanzees and bonobos are almost identical in the amount of time they spend alone in all other contexts (31.1% and 31.8% respectively for both sexes; 32.8% and 29.9% respectively for just females Figures 3 and 4). The trends for both sexes and for just females of each species remained consistent across behavioral contexts (Figures 3 and 4), with gorillas consistently being the most likely to alone in all contexts.

## **Discussion**

When summarizing the amount of time each individual spent in every behavioral context coded for, we found that all three species spent similar percentages of their time in similar contexts (i.e. every species spent slightly less than a third of their time feeding/foraging). Additionally, when looking at feeding/foraging, resting, and all other contexts, we found that all three species were spending similar percentages of their time in each of these three categories. However, note that some of the most common “other” behaviors differed across the three species (i.e. grooming was far more common in chimpanzees and bonobos than in gorillas) (Figure 1). These data suggest that differences in activity budgets between the species are small, and therefore likely do not account for differences seen here in sociality. We found that there was a significant interaction between species and behavioral context in both sexes and in just females ( $p=0.002$  and  $p=0.017$  respectively) when contexts were pooled into feeding/foraging, resting, and other categories (Figures 3 and 4). Gorillas and bonobos seem to be similar in their social tolerance when all contexts are considered (Figure 2; 68% and 52% time alone respectively). However, both species spend more time alone than expected, suggesting that THV dispersal in the wild may actually select for gorillas and bonobos to be more spread out while feeding.. These data seem to support the hypothesis that bonobos and gorillas would be more similar to one



another than either would be to chimpanzees in terms of their sociality. However, the similarity is unexpected as it was hypothesized that bonobos and gorillas would both be spending *more* time in close proximity to conspecifics than chimpanzees (Figure 2). Additionally, when the specific behavioral contexts are examined, the species differences are more complex. As expected, the captive bonobos in this study showed that they are the most tolerant (as evidenced by proximity of conspecifics) of the three species when feeding, however, gorillas were the least tolerant (Figures 3 and 4). These results are unexpected given the documented similarities in social and foraging characteristics of bonobos and gorillas (Yamakoshi, 2004; Malenky *et. al*, 1994). Based on supposed similarities in group cohesiveness, it was hypothesized that bonobos and gorillas would be similar in tolerance across contexts, but specifically while feeding/foraging when competition is likely the highest. While captive bonobos do spend less time alone in feeding/foraging contexts than the other two ape species, gorillas spend the most time alone. This is surprising given the proposed relationships between the feeding ecology of gorillas and within-group cohesion (i.e. THV foraging allows for large, cohesive groups) (Yamagiwa, 1999). However this finding does seem to reflect disparities in the original THV hypothesis. The chimpanzee population in this study did spend more time alone than bonobos, as expected, however they spent less time alone than gorillas (Figures 3 and 4). Gorillas and bonobos were similar in resting contexts, however chimpanzees seemed to be more tolerant than the other two species in this category (Figures 3 and 4). This may reflect the intensity of fission-fusion in chimpanzees, causing relatively high amounts of time alone while feeding, but leading to low amounts of time alone in other contexts. In this way, these data imply that chimpanzees do in fact regulate competition while feeding through use of fission behaviors, but then re-associate with conspecifics when the potential for competition decreases (i.e. in resting contexts).

A significant interaction was also found when considering just the female subjects of each species (Figure 4), with trends within each behavior remaining consistent with what was found when

both sexes were analyzed. However, again, the pattern of results observed in female gorillas was unexpected given that ecological characteristics of the great apes have been hypothesized to related to differences in female-female bonds, and these types of bonds have been correlated to the degree of feeding competition present (White, 1998). In this way, gorilla females were reasoned to be similar to bonobos in their amount of social tolerance as a result of the similarities in their diets and foraging profiles, but the data presented here do not support this claim. Since relatively lower levels of competition in bonobos and gorillas have been hypothesized to be a result of their ability to use THV as a supplementary food source (Malenky and Stiles, 1991; Kano, 1983; Hashimoto *et. al*, 1998; Malenky *et. al*, 1994), we expected that group tolerance in these species would reflect this even in captive populations. Though captive studies do not allow for natural environmental conditions, they do allow for control of group size, feeding schedules and diet, and focal individual visibility, making them ideal for direct comparisons of multiple species. As such, species-typical characteristics of social behavior should become apparent even in captive populations due to the ability to keep variables consistent across populations. The bonobos in this study were more tolerant in feeding contexts than chimpanzees as evidenced by proximity to conspecifics during feeding/foraging (bonobos spent 66% of their time alone when feeding, whereas chimpanzees spent 71% of their time alone when feeding). However, gorillas were not similar to bonobos in this regard. In fact, gorillas were the least tolerant of conspecifics during feeding/foraging (spending 84% of their time alone in feeding contexts) (Figures 3 and 4). These findings suggest that the maintenance of social tolerance in stressful situations (i.e. competitive feeding contexts) may have been selected for in bonobos, as suggested by the literature, but that other factors may be accountable for the gregariousness that has been suggested for gorillas.

The THV hypothesis, states that the use of THV as a food source in bonobos and gorillas has helped to facilitate social bonding and group cohesion, specifically among females, in bonobos as well as in gorillas (Wrangham, 1986). Additionally, this has been suggested as the ultimate cause of chimpanzee

and bonobo social differences. This is significant given that similarities have been identified in both the social structure (i.e. group cohesion, gregariousness of conspecifics, large groups) (these data; Yamakoshi, 2004; Malenky *et. al*, 1994; White and Chapman, 1994) and in the ecological and foraging profiles (Malenky *et. al*, 1994 in Ndoki Reserve bonobos; Furuichi, 2009; White and Wrangham, 1988) of bonobos and gorillas, two species that do not have overlapping habitats in any part of their range. Data directly comparing the socio-ecological characteristics of bonobos and gorillas are relatively sparse, and those comparing all three African Great Ape species are practically nonexistent (but see Malenky *et al*. 1994 for a comparison). However, indirect comparisons suggest that similarities and differences in the socio-ecology of bonobos and gorillas may be a result of the presence of gorillas in chimpanzee, but not in bonobo, habitats (Malenky and Wrangham, 1994). If this is the case, it is possible that the presence of gorillas in chimpanzee habitats may correlate with the divergence of social behaviors in bonobos and chimpanzees (Yamakoshi, 2004; Malenky *et. al*, 1994). Extensive degrees of sympatry between gorillas and chimpanzees likely provided a competitive pressure for the development of contrasting socio-ecological behaviors as a way to promote niche separation. It is likely that fission-fusion, frugivory, and general aggressiveness in chimpanzees, and group cohesion, frugivory/folivory, and general gregariousness in gorillas are strategies selected for as a result of the potential for competitive exclusion in habitats where the two apes have historically been sympatric (Tutin *et. al*, 1991). Contrastingly, as bonobos have likely been separated from gorilla habitats for much of their evolutionary history, and have therefore been free of potential competition with a close phylogenetic relative, it is likely that continuation of specialization in their socio-ecological characteristics never had to occur (Yamakoshi, 2004). In fact, stark differences in the social behaviors of chimpanzee subspecies that live with gorillas (central and eastern chimpanzees) and those that do not (western chimpanzees) seem to support this hypothesis, with western chimpanzees seemingly exhibiting more “bonobo-like” socio-ecological traits (Yamakoshi, 2004). Thus, chimpanzees that are sympatric with gorillas are likely limited in their ability to

feed on THV, whereas bonobos and western chimpanzees are not. However, the validity of the THV hypothesis, as it relates to the relationships between gorilla and bonobo sociality and ecology, has been heavily debated in the literature (Yamakoshi, 2004). Critical data on bonobo ecology are still missing, as are data on western lowland gorillas. These data are essential to evaluating the validity of the THV hypothesis because western lowland gorillas are the gorilla subspecies that experience the most significant habitat overlap with chimpanzees. Therefore, direct comparisons of chimpanzees, western lowland gorillas, and bonobos likely have the highest potential to reveal the impact of THV on social behaviors. Moreover, much of what has been documented about gorilla sociality, and much of what the THV hypothesis has been based on, is rooted in data collected from habituated groups of mountain gorillas. This subspecies is almost entirely folivorous and does not overlap at all with chimpanzees. Western lowland gorillas, however, exhibit high variability in their feeding patterns compared to mountain gorillas and feed much more commonly on fruit (Yamakoshi, 2004). Group cohesion in western lowland gorillas is still thought to be facilitated by the presence and utilization of THV, and bonding among group members is thought to be high. However, references to what constitutes a bonded western lowland gorilla group are rare in the literature, as are definitions of proximity. In this study, proximate social partners were classified as those that were physically touching or within 1.5 meters of the focal individual. It is possible that this definition of closeness may be too restrictive to provide a picture of social tolerance. However, using such a restrictive definition should, in fact better reflect social tolerance if individuals of a group are actually within the 1.5 meter range (i.e. within arms reach of one another).

Wrangham (1986) argues that gregariousness within gorilla groups is less costly than in more frugivorous apes as a result of their use of THV as a fallback food. This claim has held true throughout the literature for mountain gorillas, but the effect of increased levels of frugivory in western lowland gorillas has raised questions about the validity of this claim for within-group social organization of this

subspecies (Watts, 1996). Therefore, the data presented here may reflect differences in mountain gorilla and western lowland gorilla sociality and may reveal some of the weaknesses of the THV hypothesis. Additionally, if the ecology of western lowland gorillas is considered, it is possible that this subspecies may actually be less tolerant than chimpanzees and bonobos (as is suggested in the data presented here). Chimpanzees maintain a consistent uptake of ripe fruit year round, presumably forcing them into individual fruiting trees. Though foraging parties are small in these conditions, it is likely that the distribution of individuals into one or a few fruiting trees has led to the need to tolerate a small amount of select individuals in close proximity. Western lowland gorilla groups, however, have been documented as being much larger on average than chimpanzees, and feed on THV when fruit is scarce. Therefore, it is likely that, though these large groups are cohesive (i.e. they do not fission-fusion), spread between conspecifics is probably high as a result of the distribution of food sources. This has been suggested to be the case when fruit is seasonally scarce, when western lowland gorillas expand their diet and decrease their range. In these conditions, gorilla groups may either crowd or disperse based on the distribution of food (Yamagiwa, 1999). In this way, it is likely that western lowland gorillas actually maintain the cohesion of their groups by increasing the distribution of individuals (e.g. inter-individual distances) when the quality of food is low.

Comparing phylogenetically close species that differ in the amount of competitive pressure that they have historically experienced; as central chimpanzees, western lowland gorillas, and bonobos do; may help to reveal ancestral traits common to all three species. Some 6-10 million years ago (Glazko and Nei, 2003), during the climactic changes of the Tertiary and Quaternary Periods (Yamagiwa *et. al*, 1996), the *Gorilla* genus split from the evolutionary line leading to humans. This split likely led to specialization in the social and ecological strategies observed in the *Pan* and *Gorilla* lineages in areas where the two genera overlapped. It is possible then, that the continued habitat overlap of western lowland gorillas and central chimpanzees led to further specialization in their socio-ecological strategies, leading to the

extremes observed in current populations. It is therefore equally possible that the freedom of this overlap in bonobo ranges provided no need to specialize any further, but instead allowed for the ability to begin to revert back to traits that may be characteristic of a common ancestor to all three species. This possibility may explain the parallels seen in social and communicative behaviors, and in the foraging profiles that exist between chimpanzees, bonobos and gorillas (i.e. bonobos are more similar to chimpanzees in communicative strategies (Pollick and de Waal, 2007) but more similar to gorillas in ecological profiles (Yamakoshi, 2004)). Similarly, it may reflect the stark difference presented here in the social characteristics of captive western lowland gorillas, chimpanzees, and bonobos.

The behavioral data collected here represent a small portion of a comparison in the socio-ecology of the three species. However, in order to more rigorously test the effect of low quality food (resembling THV) and high quality food (fruits) in differing distributions on the social strategies of each species, it is necessary to manipulate these variables.

Size and quality of food patches in the wild have been proposed by many researchers to be the causal factor leading to developments of evolutionarily stable foraging strategies among the great apes as well as among most other animal species, have been attributed to social characteristics of those species, and have been identified in theoretical studies (Snaith and Chapman, 2005 in red colobus monkeys; Davis *et. al*, 2011 in walnut flies; Ruxton *et. al*, 2005 theoretical foraging; Newton-Fisher *et. al*, 2000; Chapman *et. al*, 1995). Therefore, the most accurate way to compare socio-ecological behavior among these three ape species is likely to experimentally manipulate the quality and distribution of food sources to reflect wild patterns while keeping all other variables as constant as possible. The current data are lacking, however, in comparing the responses to changing dispersal and quality of food, as well as the effects of aggression between individuals on the behavior of the African Great Ape groups. Since differences in the quality and dispersal of food exploited by each of the African Great Apes is a major contributing factor to the THV hypothesis it is necessary to compare the three species with respect to

their behavioral responses to these variables. However, this is a difficult task in AZA accredited zoos, due to the inability to experimentally manipulate predetermined diets and foraging schedules/food distributions. In order to reconcile this, we sought to add theoretical analyses of variability in food patch size/quality and encounter rate to the existing data presented here in order to simulate the scenarios that best reflect the natural habitats of each species. Combining the behavioral data present above with theoretical results of the behavioral responses of each species in terms of variability in food patch size, quality, and dispersal should then provide a well-rounded picture of how chimpanzees, bonobos, and gorillas compare to one another in their socio-ecological behaviors.

### **3- Ecological Modeling: Introduction**

#### *Theoretical Modeling of Responses to Changes in Food Quality and Encounter Rate*

As a compliment to the above behavioral comparisons of chimpanzees, bonobos and gorillas, mathematical modeling approaches were used to infer evolutionarily stable strategies (ESS's) of aggressive, or presumably more chimpanzee-like, individuals and affiliative, or more gorilla-like, individuals in varying ecological conditions. Food distribution and quality were difficult to manipulate in the zoos in which this study was performed, therefore theoretical analyses of behavioral changes to variations of these conditions were necessary to provide a complete comparison of the strategies of the three African ape species. The model used here is a variation of a model introduced in Dubois *et al.* (2003). In the Dubois *et al.* model, a manipulation of the classic hawk-dove foraging game was used to simulate ESS's of resource defense in group foraging contexts. However, their model placed emphasis on simulating the effect of the finder's share, or the amount of the initial food patch that the finder gets before another individual arrives, on ESS's. We instead sought to conceptually map the environmental conditions of a gorilla-like and chimpanzee-like world onto Dubois *et al.*'s existing model and investigate ESS's in terms of the size/quality of food patches and the encounter rate of those patches. In this way,

the re-exploration of the Dubois model provides another layer to the comparison of African Great ape behavior as it relates to changing environmental conditions. In these models, when the term “payoff” is used, we are referring to the expected advantage of each individual playing a hawk or dove, or being chimpanzee-like or gorilla-like.

In group living animals, like primates, social foraging often leads to either scramble or contest competition in order to gain access to desired food in clumps found by other individuals. This type of foraging behavior commonly causes fluctuations between aggressive and peaceful interactions over access to resources within foraging parties. These factors have historically been modeled, in primates as well as in most other vertebrates, using two main approaches; an optimal foraging outlook on resource defense and a game theoretic outlook (Dubois *et. al*, 2003). The model presented here takes the approach of the latter. Most existing models allow individual payers in the system to be a producer versus a scrounger, the equivalent of a finder or a joiner, a hawk versus a dove, or some combination of these strategies (Barta and Giraldeau, 1998; Ruxton *et. al*, 2005; Dubois *et. al*, 2003). Though all of these models address some critical aspect of an ape foraging world and can be used to some extent to infer relationships of individuals in our system, they do not explicitly address impact of changes in food quality/dispersal. For example, Barta and Giraldeau (1998) address how social dominance when foraging affects the defense of resources. Though their model addresses some aspects of the effects of dominance hierarchies in great ape foraging units, it does not include the possibility of large groups, competitors with different levels of aggression, or variations in abundance and divisibility of food items. Similarly, Ranta *et. al* (1995) use the notion of information sharing among conspecifics to model interactions between unequal competitors, finding that foraging groups should be separated by foraging ability. Again, their model gets at a critical aspect of ape foraging, but does not specifically address the effect of abundant or lower quality food. Lastly, Ruxton *et. al* (2005) introduce models of situations that predict the critical distance between food patches at which it is stable for conspecifics to join already



occupied food patches, a prediction that may mirror fission-fusion behavior in chimpanzees and bonobos. Ruxton *et. al's* model also addresses the effect of patchiness of resources, but does not take into account the quality or size of those patches.

Ecological variables relevant to a great ape foraging system are included in all of the above models however, they do not address potential seasonality in resources by explicitly manipulating changes in patch quality, size, or dispersal (Ruxton *et. al*, 2005). In some producer-scrounger models, such as those presented in Barta and Giraldeau (1998), it has been found that players with similar competitive abilities should not alter their role as either producer or scrounger, but all players should instead play these roles equally. However, when competitive differences become larger, more interesting effects on the behaviors of producers and scroungers are seen, with dominants playing scrounger and subordinates playing producer (Barta and Giraldeau, 1998). A system such as this seems to parallel the real world strategies of great apes, specifically bonobos, that have clear differences in dominance among male and female group members. Though each of these types of models provide a clear framework for the development of a new model to represent a great ape foraging system based on existing literature and empirical data of great ape socio-ecology, they do not overtly address the two variables of interest for our system. Therefore, combining aspects of these models and incorporating new parameters and variables provides a useful compliment to the behavioral data collected above.

As such, we chose to use the hawk-dove foraging model introduced in Dubois *et. al* (2003) as a template for additional exploration. The basic hawk-dove model sets two potential strategies against each other in a foraging scenario. Each player in the system can either be a hawk (or an aggressive individual) or a dove (a non-aggressive individual) and can meet under differing combinations of parameters. The model itself evaluates the ESS's of each player under combinations of these parameters and different strategies of the other player in the system. For example, if two hawks meet in the model, there is an aggressive interaction and each hawk expects to gain half of what is left in the patch minus

the cost of aggression and the length of the fight. If a hawk and a dove meet, the dove is displaced and the hawk gains access to the resource without incurring the cost of a fight. If two doves meet, the resource is shared because neither individual chooses to be aggressive (Dubois *et. al*, 2003). This basic framework was chosen as a model to interpret in further detail because it allows for interaction between an aggressive individual, a strategy that mirrors chimpanzees, and an affiliative individual, a strategy that seems to be more gorilla-like, and to some extent more bonobo-like. Rather than using solely game theory, Dubois *et. al* (2003) combined their model with resource defense theory to determine the ESS's of hawk joiners and finders and dove joiners and finders in varying ecological conditions. Their model expanded on one presented in Sirot (2000) which involved players with equal competitive ability competing only in pairs. However, as most real world competitive interactions involve asymmetric players and clumps of food, Dubois *et. al* added competitive ability and encounter rate into their model. Dubois *et. al* present several models that introduce various costs to finder and joiner hawks and doves, however we chose to focus on manipulating the outcomes of just one of their models; a two-forager hawk-dove game with temporal costs. Here, the effect of patchiness of resources and the amount of the food patch that the finder gets is addressed, but the size or quality of the food patch as a variable is not manipulated. Therefore their existing model does not specifically discuss the impact of environmental conditions characteristic of a great ape world on ESS's. Thus, we chose to use this model as a framework and manipulated encounter rate and food patch size to better reflect our system.

The model as developed in Dubois *et. al* (2003):

The two-forager game involves conditions of the environment that affect the ESS's of players that can either be a finder, the individual that comes in contact with a patch of food first, or a joiner, the individual that comes to the patch after the finder has already consumed some portion of the patch. Each of these individuals can choose to be either an aggressive hawk, or a non-aggressive dove. The

theoretical world described in Dubois *et. al* begins with a food patch (F) that is encountered by a finder at some rate ( $\lambda$ ). At this food patch, the finder gains a finder's advantage (a) before the joiner arrives at the patch. With the arrival of the joiner there is the potential for several different outcomes based on the strategies played by each individual. Both individuals can play hawk (H,H), in which case there is a fight with an energetic cost (C) to both hawks that lasts for a set period of time (t). A hawk finder can encounter a dove joiner (H,D), in which case the finder gains the finder's advantage (a) and the joiner is aggressively displaced from the patch with no cost of fighting. A dove finder can encounter a hawk joiner (D,H), in which case the finder still gains the finders share (a) but is then displaced by the joiner who gains access to the patch at (F-a). Finally, both individuals can play dove (D,D), in which case the finder gains the finder's share (a) and the remainder of the patch is split between the finder and the joiner. Note that in this system the finder's strategy is depicted by the first letter in parentheses and the joiner's strategy is depicted by the second letter. Definitions of these variables and parameters can be found in Table 5.

Combining these variables and parameters into expected payoffs for a finder and a joiner when they are either a hawk or a dove yields a matrix of potential interactions in the Dubois *et. al* hawk-dove game (Figure 5).

Based on this payoff matrix from Dubois *et. al*, if the strategy of the joiner is considered, when the finder plays a hawk the joiner should also play a hawk when  $E_J(H, H) > E_J(H, D)$  (the fitness of each individual is represented by  $E_{F \text{ or } J}$ ). Similarly, when considering the strategy of the finder, when the joiner plays a hawk the finder should also play hawk when  $E_F(H, H) > E_F(D, H)$ , and so on for all scenarios. Based on this method of pairing the strategies of finder and joiner in all possible combinations of the opponent's strategy, thresholds at which the strategies of each individual change in relation to the variables of interest can be determined. By setting the possible decisions of a joiner playing a hawk

or a dove when the finder is a hawk equal to each other, the joiner paying a hawk or a dove when the finder is a dove equal to each other, and so on for the strategies of the finder we can determine the ESS's of each player. In doing this, the payoff matrix yields:

1. (H,H) as an ESS when  $a < F - 2C$  and when  $\lambda < (F - a - 2C)/2at$ 
  - Or, it is stable for both individuals to play hawk when the amount of energy expended in a fight is less than what is left in the food patch after a fight, and when the encounter rate with other food patches is less than the cost incurred for taking the time to fight. In these cases, it makes sense for individuals to be aggressive because the expected payoff to them winning a fight and gaining what is left in the food patch is greater than the cost of the fight itself.
  
2. (D, H) as an ESS when  $a < F - 2C$  and when  $\lambda > (F - a - 2C)/2at$ 
  - That is when the amount of energy expended in a fight is less than what is left in the food patch after a fight and when the encounter rate of other food patches is higher than the cost incurred by taking the time to fight. In these cases it pays for the finder to be a dove and gain the finder's advantage, then leave before an aggressive encounter because the probability of finding another patch is high
  
3. (H,D) as an ESS when  $a < F - 2C$ 
  - This strategy is only stable when the amount of energy expended in a fight is less than what is left in the patch after the fight. In this case it makes sense for the finder to be aggressive because the cost of aggressiveness is less than what it gains from winning the patch.

These equations create thresholds at which the ESS's of finder and joiner strategies change when manipulating "a" and "λ" while all other parameters in the model are held constant. A recreation of Dubois *et. al's* figure representing this is shown in Figure 6.

This model predicted that the emergence of a dove-dove foraging scenario is never an ESS, and that both individuals playing hawk is only stable in a narrow range of conditions. This is because in these conditions, the time spent fighting is more costly than the time needed to find another clump of food

without a fight. The threshold at which the ESS for the finder switches from a hawk to a dove is represented by the curve  $(F - a - 2C)/2at$ . In this game, making the finders advantage larger will change the strategies of the players only when there is a low encounter rate of food patches. Therefore, the model predicts increased density of competitors, or a smaller finders advantage, will lead to an increase in aggression within groups, as will increasing the richness of patches.

The results of Dubois *et. al's* model address some crucial aspects of a hypothetical great ape world. For example, based on accounts of gorilla and chimpanzee social structure and aggression, the hawk-dove game maps well on to the interactions we would expect to see in groups of gorillas and chimpanzees. In general, gorillas, and to some extent bonobos, tend to be less aggressive, more gregarious, and more tolerant of conspecifics in close proximity, especially while feeding. While chimpanzees exhibit high levels of aggression causing them to split into smaller foraging groups in order to regulate within-group competition (White, 1996; Wrangham *et. al*, 1996; Yamakoshi, 2004). In this way, using a hawk-dove type game theory model provides a framework with which to simulate interactions of aggressive, or chimp-like, individuals and affiliative, or gorilla-like, individuals in changing ecological variables. Similarly, the above model manipulates the encounter rate of food patches as well as the finder's advantage before a joiner arrives, suggesting influences of patchiness and group size on the decisions of finders and joiners. However, the model does not explicitly plot the effects of fluctuating food clump size (F) in relation to the encounter rate of food patches ( $\lambda$ ), though it is suggested that increasing clump quality and decreasing encounter rate should increase aggression in a group foraging context. This suggestion seems to apply well to what would be expected in great ape environments. However, plotting the results of the Dubois model in terms of (F) and ( $\lambda$ ) specifically may elucidate how food availability, size, and quality of food clumps that change seasonally in the wild should effect decisions of individuals to be aggressive or not (Furuichi *et. al*, 2001). We therefore sought to explore Dubois *et. al's* existing model further and manipulate the payoffs presented in it with respect

to food clump size and encounter rate, keeping “ $C$ ”, “ $t$ ” and “ $a$ ” constant. In this way, we aimed to simulate environmental conditions that have been documented as causal factors leading to social characteristics of chimpanzees, gorillas, and bonobos by mapping these conditions onto Dubois *et. al*’s existing model. Figure 7 shows our assumed environmental conditions applying to chimpanzee and gorilla-like worlds.

#### Exploration of the Dubois *et. al* model with a great ape foraging world in mind

In order to simulate the hypothetical habitat structures of the African Great Apes, the interest of our modified system shifted from modeling the effects of finder’s advantage ( $a$ ) and encounter rate ( $\lambda$ ) on the decisions of finders and joiners in a given system to modeling behavioral responses of aggressive and non-aggressive individuals to fluctuations in food clump size ( $F$ ) and encounter rate ( $\lambda$ ). In this interpretation, chimpanzee-like individuals (or hawks) were pitted against gorilla-like individuals (or doves) in varying values of ( $F$ ) and ( $\lambda$ ) with all other parameters of the Dubois *et. al* model being held constant. Based on knowledge of chimpanzee and gorilla ecology and social behavior the Dubois model was explored in terms of ( $F$ ) and ( $\lambda$ ) in order to mirror environmental conditions ranging from high quality, clumped food to low quality, dispersed food. As such, with further explorations of the results of the Dubois *et. al* model we sought to address 1) What strategies of players are evolutionarily stable when the size/quality of a food patch changes? 2) What strategies of players are stable when the encounter rate of food patches changes? 3) Are these strategies consistent with what is expected based in great ape socio-ecology? 4) Do responses to fluctuations in these variables correspond to the behavioral data collected?

Gorilla groups, and to some extent bonobos, often chose to modify group ranging patterns and dietary preference in response to changes in seasonal availability of preferred fruit, expanding their dietary breath to encompass more diverse food items and increasing resource acceptance in the

presence of conspecifics (Davis *et. al*, 2011; Tutin *et. al*, 1991; Malenky *et. al*, 1994). In contrast, chimpanzees maintain a consistent uptake of fruit and instead expand the size of their day ranges and reduce the size of feeding parties to regulate competition among conspecifics (Newton-Fisher *et. al*, 2000; White and Wrangham, 1988). These species' characteristics compliment the idea that the distribution and abundance of food items determine whether a species will exhibit aggressive, contest completion or peaceful, scramble competition (Snaith and Chapman, 2005). As a result of the socio-ecological characteristics of the three African great apes in this study, and the predicted effects of manipulating the availability and quality of food items we hypothesized that:

- 1) *Individuals should be chimpanzee-like (or aggressive/hawk-like) in nature when the size/quality of food patches is high, but the encounter rate of those patches is low.*
- 2) *The ESS of individuals should be gorilla-like (or affiliative/dove-like) when the encounter rate of food is high, but the quality of that food is low.*

### Methods

All equations of expected payoffs presented in Dubois *et. al*'s model were kept the same, and no new parameters or variables were added to the existing model. Each individual could still play hawk (or chimpanzee-like) or dove (gorilla-like) as in the Dubois *et. al* model. The payoff matrix of potential interactions is the same as the original Dubois matrix and is presented in Figure 5.

As in the Dubois *et. al* model, we then determined at what combination of parameters the finder's (or the initial individual at a patch) strategy was evolutionarily stable as a hawk (or chimpanzee-like individual) when the opponent was also a hawk. The same comparison was done for the strategies of each individual in all possible combinations of strategies, listed below. Any further reference to the initial individual in the patch is the equivalent of the finder of that patch, similarly, any reference to the opponent of that patch is the equivalent of the joining individual.

- 1)  $E_F(H, H) > E_F(D, H)$
- 2)  $E_F(H, D) > E_F(D, D)$
- 3)  $E_J(H, H) > E_J(H, D)$
- 4)  $E_J(D, H) > E_J(D, D)$

In each of the above scenarios, the payoffs to each individual were set equal to each other using the payoff matrix (Figure 5) and the variables of interest (F and  $\lambda$ ) were solved for accordingly.

EXAMPLE 1:  $E_F(H, H) > E_F(D, H)$

-Setting these two strategies of the finder equal to each other yields:

$$[(F+a)/2-C]/(1+\lambda t) > a$$

Solving for F

$$F > a + 2a\lambda t + 2C$$

So the initial individual should always play hawk, or be chimpanzee-like, when the opponent is also playing hawk when the total size of the food patch is greater than the cost of two aggressive individuals fighting. This was done for all combinations of strategies listed above.

## Results

### *Analysis of expected payoffs*

Based on the combination of scenarios described above, when the opposing individual is a hawk, the initial individual should also be hawk when  $E_F(H, H) > E_F(D, H)$ -or when  $F > a + 2a\lambda t + 2C$ . When the opposing individual is dove, the initial individual should be hawk when  $E_F(H, D) > E_F(D, D)$ -or when  $F > a$ , therefore the initial individual should always be a hawk when the opponent is a dove because the initial size of the patch must be larger than the finder's advantage. When the initial individual is a hawk, the opposing individual should also be a hawk when  $E_J(H, H) > E_J(H, D)$ -or when



$F > 2C + a$ . When the initial individual is a dove, the opposing individual should be a hawk when  $E_j(D, H) > E_j(D, D)$ -or when  $a < F$ , therefore the opposing individual should always be a hawk when the initial individual is a dove because the size of the initial food patch must be greater than the finder's advantage. These analyses gave rise to four possible stable strategies in the plane of " $\lambda$ " versus " $F$ " (Figure 8)

(H,H) is stable, or when the joiner is a hawk, the finder will gain a higher payoff as a hawk than as a dove when  $F > a + 2a\lambda t + 2C$  and  $F > 2C + a$

(D,H) is stable, or when the joiner is a hawk, the finder will gain a higher payoff as a dove than as a hawk when  $F < a + 2a\lambda t + 2C$  and  $F > 2C + a$

(H,D) or (D,H) are stable when  $F < a + 2a\lambda t + 2C$  and  $F < 2C - a$

### Discussion

In the above model, we expanded on the results presented in Dubois *et. al* (2003) in order to infer the evolutionarily stable strategies of aggressive and affiliative individuals in changing ecological conditions. Like Dubois *et. al*'s model, the expansion predicts that two affiliative individuals (D,D) will never be an evolutionarily stable strategy when just the encounter rate and the size of food patches are manipulated. Based on the socio-ecological characteristics of chimpanzees, gorillas, and bonobos, we expected that at low encounter rates and small food patch sizes we would see an emergence of peaceful behavior in both players of the game. However, this was not the case in the Dubois model. Instead, peaceful behavior of the initial individual was an ESS when the size of food patches was low, as expected, but remained the ESS across a range of encounter rates. These data somewhat reflect what we would expect based on real world observations, however it is possible that changing the size of the food patch does not sufficiently alter the behavior of the individual enough to provide a complete picture, and therefore adding a food quality variable may be necessary. In addition, we found two

possible ESS's at extremely low patch sizes, but across a range of encounter rates. At these levels, it was stable for the initial individual to be chimpanzee-like when the opponent is gorilla-like (H,D) but also could be stable for the opponent to be chimpanzee-like when the initial individual is gorilla-like (D,H). These strategies seem to contradict each other and suggest that an aggressive displacement is a stable strategy even in conditions when food patches are small but readily available, potentially implying that the benefit of an aggressive displacement outweighs the opportunity to find a new patch of food even when that opportunity is high. Based on predictions of the ecological constraints model and optimal foraging theory, the emergence of these two possible strategies at that combination of parameters seems odd (Snaith and Chapman, 2005). It is, however, possible that these two ESS's exist in this model as a result of the payoff equations used, and a (D,D) ESS may never emerge in this model, even though it makes sense that it should. In order for a (D,D) ESS to emerge, it is likely that there would have to be some cost to chasing off an opposing individual, which this model does not account for. However, it is possible, that with this cost it may be stable for both individuals to then be affiliative in order to avoid an additional cost when food quality is low.

Thus, the ultimate outcome in this region is still somewhat unclear, but our results do suggest that gorilla-like traits emerge at the expected quality of food, just not at the expected encounter rate in our manipulation. As the model is right now, there is likely a cycle of strategies at this combination of variables, meaning one strategy of players is more common initially and then the strategy gradually begins to change. In other words, in a world full of aggressive individuals it makes sense to be an affiliative individual, but as this changes and there is a surplus of affiliative individuals it then becomes stable to be aggressive. In this region, if there is a fight, the cost of the fight would be greater than the size of the food patch, therefore gorilla-like individuals that mutually share resources should become an ESS. Additionally, our model does predict ecological conditions in which we hypothesized that chimpanzee-like behavior would be an ESS. In large patches with relatively low encounter rates,

chimpanzee-like behavior of both players emerges as an ESS, suggesting that it is beneficial to defend a large, or potentially high quality, patch when those kinds of patches are scarce. In other words, to justify fighting when there is a high encounter rate of patches, the patch to be defended must be very high quality ( $F > a + 2a\lambda t + 2C$ ). In contrast, at very low encounter rates and relatively low patch size, it still pays to fight because the probability of finding another patch is so low. This reflects what has been observed in wild ape populations and correlates well with predictions that highly frugivorous primates will compete for high quality, patchy foods (Snaith and Chapman, 2005). Region 2 of our figure also reflects a somewhat unclear area of behaviors, however this region could potentially reflect scenarios in which bonobo-like behavior becomes stable. Barta and Giraldeau (1998) found that dominant individuals in a group should play scrounger (or the equivalent of a joiner) while subordinate individuals should play producer (or finder) when resources are patchily distributed. Their model assumed that high ranking individuals are competitively superior and thus should be the ones in a group foraging scenario that play scrounger. Barta and Giraldeau's model also predicted that group cohesion can only be maintained to a certain degree of competitive asymmetry in a group, after which it pays for subordinates to break off and form new groups. This type of model seems to reflect the fission-fusion behavior of chimpanzees and bonobos and may specifically apply to bonobos in the context of the results presented here. In bonobos, the female is the dominant sex class and males often forage alone (White and Chapman, 1994; Malenky and Stiles, 1991), suggesting that females are likely the scroungers when food is clumped while males are the producers. The results presented here reflect the possibility of this occurring in Region 2 (Figure 8). This area of the figure represents a combination of parameters that are an intermediate between what was expected for chimpanzees and gorillas, a space where we would expect to see bonobo-like behavior develop. In this area, (D,H) is an ESS, suggesting that, when the initial individual in a patch is subordinate, or affiliative, the joiner should be dominant, or aggressive. This parallels what

may be expected in a bonobo-like habitat and reflects relationships between females and males, but is tentative at this point and needs further modeling.

The two variables manipulated in the Dubois *et. al* model reflect some aspects of real-world ape ecological conditions, such as seasonal decreases in productivity of fruiting trees and highly vegetated habitats. However, as with many other models of foraging behavior, this model is restricted in addressing all of the relevant conditions needed to provide a complete analysis of behavioral responses to the variables of interest. Resource defense theory predicts that aggressiveness will be selected for when resources are patchy and high quality, and therefore dominance relationships may become important in group foraging scenarios (Barta and Giraldeau, 1998). Therefore, additional models that alter size and quality of resources, their defensibility, and costs to aggressive individual that live in affiliative worlds or needed. In addition, models addressing relationships between dominant and subordinate individuals in changing ecological conditions may be a more thorough way to simulate ape foraging behavior.

#### Adding on to the Dubois *et. al* 2003 Hawk-Dove game

Since the model utilized by Dubois *et. al* lacked any cost to a Hawk being present in a world of Doves, the occurrence of (D,D) was never an ESS in the plane of  $\lambda$ -F. Therefore, in order to explore which food-related parameters, and which representations of great ape environmental conditions, would favor the presence of Dove behavior, we introduced a “chasing cost” to the existing model. This cost is incurred only when an individual chases an opponent from a patch of food, and as such is only paid by Hawks who chase Doves from a resource. This could represent costs (e.g. energy expended or feeding time lost) of monitoring the arrival of other apes to the patch as well as displaying to or chasing the other individual. This kind of interaction does not lead to an aggressive interaction in which either of the players are injured or incur some cost of a fight, so it is not as costly as two hawks meeting. However, it

is different from Dubois *et. al*'s interactions in which, if a hawk meets a dove, the latter of the two is chased off with no cost to the hawk in terms of postponing feeding or expending the energy to chase the dove. As such, including a parameter like the cost of chasing, represented here by "z", allows for a model in which (D,D) strategies (co-feeding) might become stable in an environment where food is extremely low quality, or sufficiently abundant (as was expected in the previous model). In these environmental conditions, it could be disadvantageous for the finder to chase off another individual (for example if the cost of chasing an individual from a low quality patch is likely higher than the benefit of winning that patch. A cost such as this may help to infer costs of territoriality in primate groups.

### Model and Results

The analysis of this model, with the parameter z included, is identical to the analysis of the original Dubois model. In it, all possible combinations of interactions between finders and joiners playing hawk or dove were set against each other in order to find the ESS under that combination of player strategies and parameters, the same was done for this expanded model. A new payoff matrix, based off of Dubois *et. al*'s matrix, was constructed with the addition of z (the cost of chasing off an opponent) in the appropriate payoff cells. This new matrix can be found in Figure 9. As in the analysis of the Dubois model, all possible combinations of the payoffs to each individual in all combinations of interactions between finders and joiners were set equal to one another and F was solved for in order to determine the threshold at which the ESS of the finder or the joiner changes. Plotting the equations yielded from this analysis now draws four regions in the plane of  $\lambda$ -F. Note that the only region that was not included in the original model, R4 (Figure 10), is a result of including "z" as a chasing cost to Hawks that chose to chase Doves from a food patch. Payoffs to finders that play hawk or dove and joiners that play hawk or dove are described below.

1.  $E_F(H,H) > E_F(D,H)$

When the joiner plays hawk, the finder in a patch gains a higher fitness by playing hawk rather than dove when  $F > a + 2a\lambda t + 2C$

2.  $E_F(H,D) > E_F(D,D)$

When the joiner plays dove, the finder in a patch gains a higher fitness by playing hawk rather than dove when  $F > 2z + a$

3.  $E_J(H,H) > E_J(H,D)$

When the finder in a patch plays hawk, the joiner gains a higher fitness by playing hawk rather than dove when  $F > 2C + a$

4.  $E_J(D,H) > E_J(D,D)$

When the finder in a patch plays dove, the joiner gains a higher fitness by playing hawk rather than dove when  $F > 2z + a$

### Results

When combining the scenarios in relation to the addition of chasing cost "z" we find ESS's emerging in regions of our figure that are similar to those found in the Dubois model and in our further exploration of their model. For example, at very high "F" values, it is still beneficial for both individuals to play Hawk (H,H), when  $F > a + 2a\lambda t + 2C$ . Similarly, below this threshold, (D,H) behavior becomes stable, as it was in the Dubois model. However, when "z" was introduced as a chasing cost to Hawk players that encounter Dove opponents we now see (D,D) behaviors emerging as an ESS at extremely low "F" values, as expected (Figure 10). Additionally, this new model predicts that, in R3 (Figure 10), the occurrence of (H,D) or (D,H) each as ESS's will not always be the case. These strategies do become stable, however, when the cost incurred by chasing off an opponent is less than half of the food that remains in a patch once a joiner arrives at that patch (or when  $z < (F-a)/2$ ).

### Discussion

The original Dubois model did not predict a situation where it would be stable for both individuals to play Dove (D,D). This finding was unexpected given the affiliative relationships in folivorous primates that have been hypothesized as being a result of the abundant dispersal of low

quality food (Tutin et. al, 1991). In environmental conditions such as this, fighting for access to a patch of food is not stable because the probability of finding another patch of equal quality is high, and therefore the cost incurred by fighting is likely much higher than the benefit of winning the patch. This was not found to be the case in the original model however, but it was reasoned that the absence of a (D,D) strategy in the environmental conditions in which it would be expected was likely a result of limitations of the original model. As such, an additional cost, that of chasing an opponent from a food patch, was added to the Dubois model. This cost only applied to Hawks who encountered Doves and therefore would have to incur some loss of fitness in order to defend a food source. It was expected that introducing this cost would select for peaceful behaviors of both individuals in extremely low quality food conditions. As predicted, (D,D) behavior did emerge as an ESS when food was extremely low quality (R4 of Figure 10). Perhaps surprisingly though, this outcome was not affected by how readily available food was. In this type of environmental condition, it is no longer stable for a Hawk to chase a Dove away from a patch of food because the cost incurred from chasing is higher than the gain of co-feeding on a low quality patch. Therefore, when there is a cost of chasing off another individual, it is stable, in extremely low quality food conditions only, to avoid this cost and for all individuals to be peaceful. The occurrence of this behavior may reflect more accurately the environmental conditions in which we would expect affiliative behavior to be selected for in wild gorilla and bonobo groups. In these types of conditions, when fruit is seasonally scarce and gorillas and bonobos expand their dietary breadth to include more THV, it is thought that affiliative relationships are facilitated by the abundance of low quality food (Wrangham, 1986). Therefore, when food quality is very low, the energy expended by chasing another individual from a patch exceeds the energy that is gained from feeding on the patch and it is no longer stable to be a Hawk in a world of Doves, or similarly an aggressive individual (or chimpanzee-like) in world of affiliative (or gorilla-like) individuals.

## Summary

The data presented here indicate some behavioral similarities in bonobos and gorillas as well as stark contrasts in the same behaviors of chimpanzees. However, these data do not suggest expected parallels in the social tolerance of bonobos and gorillas during feeding/foraging scenarios. Additionally, theoretical analyses of environmental conditions where more affiliative versus more aggressive behaviors are expected to emerge as evolutionarily stable strategies mirror what have been hypothesized in chimpanzees, gorillas and bonobos. We predicted that gorillas and bonobos would show similarities in their social behaviors as a result of their shared tendencies to use THV as a fall back food in the wild in times of fruit scarcity. This adaptation has been hypothesized to be a causal factor leading to many of the sociological differences seen in all three African great apes. Gregariousness in African great ape groups, as well as the strength of female-female bonds, are both thought to be largely influenced by the distribution of food in their respective habitats. Additionally, the ability for bonobos to utilize THV as a major food source is thought to be facilitated by the lack of competition with gorillas. This absence of this pressure has likely helped lead to the maintenance of socio-ecological characteristics that are not seen in chimpanzees, probably because of the presence of gorillas in much of their range. The effects of these pressures have potentially led to a divergence of social strategies in the *Pan* genus somewhere along their evolutionary line. As a result of this, we sought to compare the social characteristics of all three species using simple methods in captive populations where ecological variables could be kept consistent. The significance of this is two-fold. First, comparing phylogenetically close species that differ in the degree of ecological competition that they experience could help to elucidate ancestral traits that may have been present before the split of the *Pan/Gorilla* lineages. Second, maintenance of variables like food distribution and group size across the three species provides for a direct comparison of the behaviors of the three species, something that has historically been difficult in wild populations. These data suggest that similarities and differences in the three African



Great Apes may be a result of their documented foraging strategies. However, the similarities that we expected to see in gorilla and bonobo social behavior did not arise, indicating that the effect of THV use in these species may not be enough by itself to account for their socio-ecological characteristics. As such, additional data on the social relationships as well as the ecology is needed, specifically as it pertains to wild western lowland gorillas. Theoretical modeling was also used here as a way to infer the effects of changing environmental factors, like food patch size and dispersal, on the behavioral responses of two individuals that could play the role of a hawk (or a chimpanzee-like individual) or a dove ( or a gorilla-like individual). The results of those models are consistent with what would be expected in the African great apes based on the literature, with aggressive strategies emerging as stable behaviors in environments high in quality of food but low in abundance of food and affiliative strategies becoming stable in environments with extremely low food quality. The implications of the models used here provide a useful compliment to the behavioral data collected and allow for a way to elucidate behaviors in changing environmental conditions that were not able to be experimentally manipulated in the zoos included in this study.

### **Integration of Thesis Research**

These data currently only address two environmental conditions that simulate a great ape foraging world, and only include behavioral analyses from captive populations. As such, more in depth modeling of additional factors that would be expected in a gorilla-like and chimpanzee-like world should be integrated into the existing model for a more complete analysis. The behavioral data presented here suggest that habitat overlap between gorillas and chimpanzees may have facilitated significant specialization in socio-ecological behavior. These data, however, should be combined with similar data collected from wild populations in areas where gorillas are sympatric with chimpanzees, where they are not, and from bonobo populations. The combinations of empirical and theoretical analyses used here provide a unique comparison of social behaviors using simple methods and infer behavioral responses to

changing environmental conditions. In this way, the comparisons presented here are unique in nature and can be integrated with future research that adds to the existing data. More importantly, they may imply traits representative of a common ancestor to the *Pan/Gorilla* lineages and could be utilized, in combination with additional data, to infer pressures leading to the evolution of social traits representative of the *Homo* genus.

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## Tables and Figures

Table 1: Summarization of the ecological characteristics of the three African Great Apes

Ecological Characteristics by Species	Chimpanzee	Gorilla	Bonobo
<b>Main Diet</b>	Fruits	Fruits/THV	Fruits/THV
<b>Fallback Staple Food</b>	Fruits	THV	THV
<b>Foraging Strategy</b>	<ul style="list-style-type: none"> <li>• Ripe fruits year round.</li> <li>• Expand home range and fission-fusion when fruit is scarce.</li> <li>• Smaller variety of fruits.</li> <li>• Large foraging range.</li> <li>• Small feeding parties.</li> </ul>	<ul style="list-style-type: none"> <li>• Opportunistic ripe fruits, consistent THV</li> <li>• Expand dietary breadth when fruit is scarce</li> <li>• Small foraging ranges</li> <li>• Larger feeding parties</li> <li>• No fission-fusion</li> </ul>	<ul style="list-style-type: none"> <li>• Opportunistic ripe fruits, consistent THV</li> <li>• Expand dietary breadth when fruit is scarce</li> <li>• Smaller foraging ranges</li> <li>• Large feeding parties</li> <li>• Fission-fusion</li> </ul>
<b>Sympatric?</b>	Yes	Yes	No

Table 2: Summarization of the social strategies of each of the three Africa Great Apes

Social Strategies by Species	Chimpanzees	Gorillas	Bonobos
<b>Dominant Sex/Social Bonds</b>	<ul style="list-style-type: none"> <li>• Male-male bonds</li> <li>• Weak female bonds</li> <li>• Dominant males</li> </ul>	<ul style="list-style-type: none"> <li>• Female-female bonds</li> <li>• Dominant silverback male</li> </ul>	<ul style="list-style-type: none"> <li>• Strong female-female bonds</li> <li>• Weak male bonds.</li> <li>• Dominant females</li> </ul>
<b>Fission-Fusion Foraging?</b>	Yes	No	Yes (but highly mixed age-sex classes)
<b>Feeding Competition/Social Aggression</b>	<ul style="list-style-type: none"> <li>• High intra-species competition</li> <li>• Small, highly aggressive foraging groups.</li> <li>• Contest competition</li> </ul>	<ul style="list-style-type: none"> <li>• Low feeding competition</li> <li>• Males protect females more often than food</li> <li>• Low feeding aggression.</li> <li>• Scramble competition</li> </ul>	<ul style="list-style-type: none"> <li>• Low feeding competition</li> <li>• Low aggression when feeding</li> <li>• Scramble competition</li> </ul>
<b>Group Structure/Size</b>	<ul style="list-style-type: none"> <li>• Small foraging groups</li> <li>• Unstable group structure and size.</li> </ul>	<ul style="list-style-type: none"> <li>• Relatively large groups</li> <li>• Cohesive and stable.</li> <li>• Modify group foraging strategies to maintain cohesion.</li> </ul>	<ul style="list-style-type: none"> <li>• Large groups</li> <li>• Cohesive and stable.</li> <li>• Modify group foraging strategies to maintain cohesion.</li> </ul>

Table 3: Possible chimpanzee, gorilla, and bonobo behaviors

Behavior	Description
<b>Affiliative Follow Give (AFG)</b>	The focal individual is following any conspecific within 1 meter. This can be done behind or beside the other individual. This behavior is considered a non-aggressive, social behavior
<b>Affiliative Follow Receive (AFR)</b>	The focal individual is being followed by a conspecific within 1 meter, as above, and does not respond to this behavior with aggression or by moving further away
<b>Copulation (CO)</b>	Actively engaging in sexual behavior or genital-genital contact with a conspecific
<b>Displaying (DI)</b>	Swaying, charging, drumming, slapping the ground or other objects, throwing etc. Should be accompanied by pilo-erection (however not in gorillas). In gorillas this can include chest beating.
<b>Feeding/Foraging (FF)</b>	Actively eating or handling food. This can include chewing or processing of food items (peeling, smashing, sucking, crushing, etc.), or can include simply holding food items in between bites or bouts of active eating. Or Actively searching for food items. For the individual to be in this context, they must not be stationary while handling food, but must be actively moving about the enclosure in search of food.
<b>Fighting (FI)</b>	Slapping, biting, hitting, or unidirectional chasing a conspecific while piloerect, or being slapped, bitten, hit or chased by a piloerect conspecific
<b>Greeting (GRE)</b>	Approaching or being approached by a conspecific that was not previously part of the interaction
<b>Groom Give (GRG)</b>	Picking through the hair or skin of a conspecific; searching for and removing debris from the body of another conspecific using the hands, feet or mouth
<b>Groom Receive (GRR)</b>	Allowing another individual to pick through the hair or skin of the focal individual and remove debris from the body of the focal individual using the hands, feet, or mouth
<b>Groom Mutual (GRM)</b>	The focal individual and one or more other individuals are performing the above behavior simultaneously on each other

<b>Locomotion (LO)</b>	Walking, running, brachiating or climbing, or another form of moving from one point to another
<b>Playing (PL)</b>	Non-aggressive interactions between two or more individuals including but not limited to tickling, wrestling, biting, sparring, bi-directional chasing, kicking, play-face, laughing
<b>Resting (RE)</b>	Sitting, laying, sleeping, or standing. The individual remains stationary during this behavior and is engaging in no other behaviors.
<b>Infant Carry (IC)</b>	Any instance of a conspecific carrying an infant (on the back, stomach, or any other body part) while locomoting
<b>Chase Give (CG)</b>	Walking, running, or brachiating closely behind (within 1 meter) another conspecific in an agonistic manor. This behavior can be performed mid-fight, or before or after an agonistic behavior (such as a slap or bite) is given. This behavior can be prolonged or can be short and used to chase a conspecific away from an area
<b>Chase Receive (CR)</b>	Any instance of being the receiver of the previous behavior
<b>Nursing (NU)</b>	Any instance of an infant actively nursing from another female, or of an adult female actively letting an infant nurse
<b>Displace Receive (DR)</b>	One or multiple individuals moving away from a space that they previously were in in response to another conspecific approaching that area
<b>Displace Give (DG)</b>	Any occurrence of an individual moving into a space (occupied by another individual) that they did not previously occupy and causing the original occupant to leave.
<b>Solicitation (SO)</b>	Gesturing, vocalizing, or performing any other behavior directed towards a conspecific that persists for more than 2 seconds and has a clear end goal (ie. Food sharing, copulation). This behavior may not always be answered with the desired response
<b>Social Inspect (SI)</b>	Staring at another conspecific within a few inches of their body. This normally occurs when the other individual is feeding, but is not accompanied by a gesture, unlike solicitation. This commonly includes staring at a female's sexual swelling etc.
<b>Other Aggressive (OA)</b>	Any behavior that could be perceived as aggressive or agonistic that is not included in this ethogram (ie. Not a fighting or chasing behavior).

<b>Other Social (OS)</b>	Any non-aggressive behavior that has not been previously described
<b>Non-Contact Aggression (NCA)</b>	Any aggressive act that does not result in the direct physical contact of two or more individuals. This can include things like charging etc.
<b>Other (OT)</b>	Any behavior that does not fall into any of the above categories
<b>Cannot be Determined (CBD)</b>	To be coded if the focal individual is out of sight at the time of the data point

Table 4: Categories of possible conspecific proximity

<b>Proximity</b>	<b>Description</b>
<b>Alone</b>	Focal individual is more than 1.5 meters away from another individual
<b>Close</b>	Focal individual is within reach of another individual such that if each individual stretched out a limb they could touch one another without relocating
<b>Touching</b>	Focal individual is physically contacting another individual

Table 5: Definitions of the parameters and variables used in Dubois *et. al's* model. In their model, “F”, “C”, and “t” are kept at constant values and the expected payoffs to the finder and joiner are evaluated in terms of “a” and “λ”.

<b>Parameter/Variable</b>	<b>Definition</b>
<b>F</b>	Initial size of the resource patch/clump
<b>C</b>	The energetic cost of two hawks fighting
<b>t</b>	The mean duration of a contest between two hawks
<b>a</b>	Finder’s advantage (amount of resource the finder consumes before the joiner arrives)
<b>λ</b>	The encounter rate of food patches in the environment



Figure 1: Total amount of time spent in the top behavioral contexts for each species. Amount of time was determined by the number of data points collected for each species in that behavioral context. Contexts with 5 or less data points were collapsed into the “other” category for each species. All other contexts with more than 5 data points are included in the figure. Grooming contexts were collapsed into one category, as were affiliative follows, displacements, infant carry, and nursing contexts. Note that the same contexts are not included for all three species.

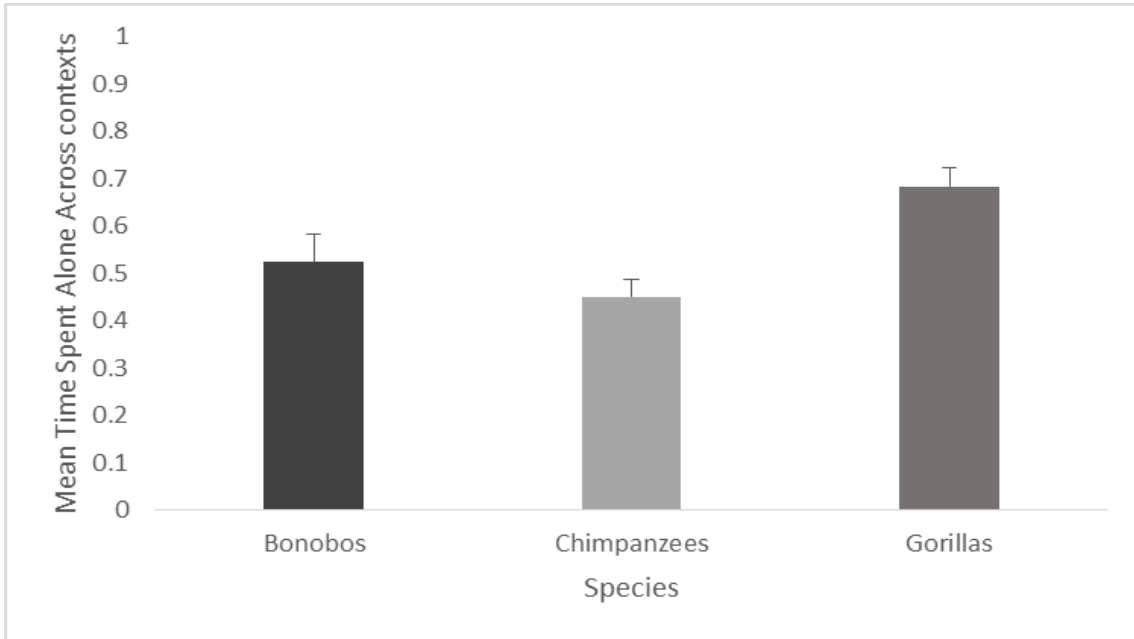


Figure 2: Average percentage of the total time spent alone per species for males and females in all behavioral contexts.

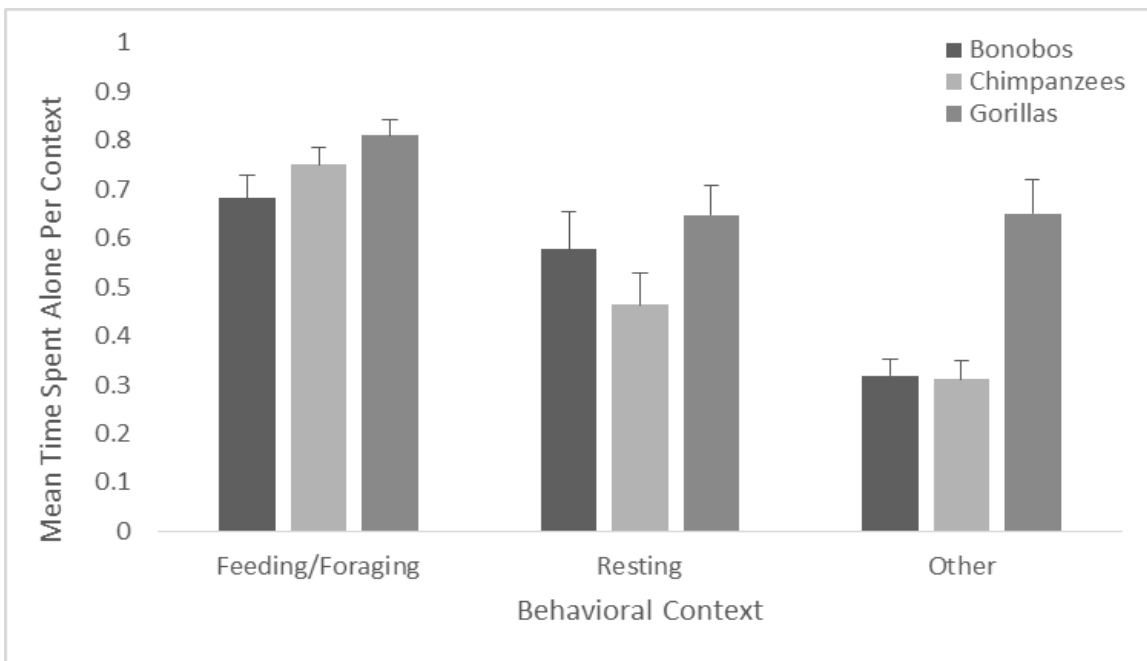


Figure 3: Average percentage of the total time spent alone by both sexes of each species in feeding/foraging, resting, and other contexts. Three chimpanzees were identified as outliers and were excluded from this analysis (n=12 (chimpanzees); n=9 (gorillas); n=10 (bonobos)). This figure does not include infants under 2 years of age as potential social partners or as focal individuals.



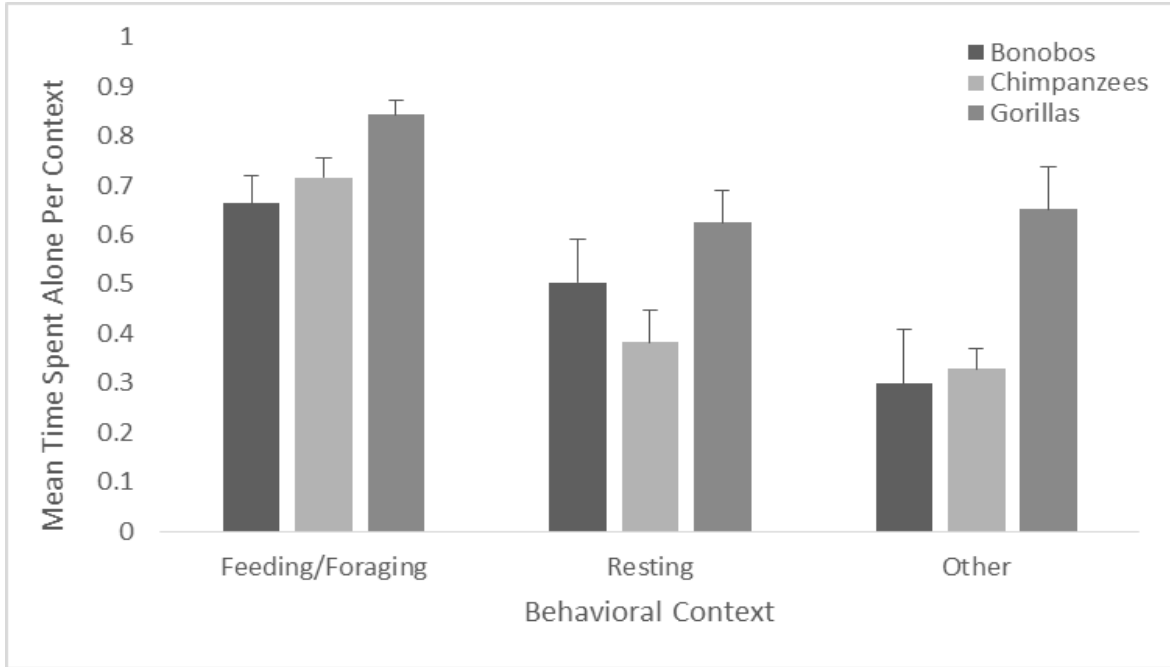


Figure 4: Average percentage of total time spent alone in just females of each species in feeding/foraging, resting, and other contexts. Two female chimpanzees were identified as outliers and excluded from this figure (n=9 (chimpanzees); n=7 (gorillas); n=6 (bonobos)). Infants under 2 years of age were not included as potential social partners.

		Choice of the Joiner	
		HAWK	DOVE
Choice of the Finder	HAWK	$E_F(H, H) = [(F + a)/2 - C]/(1 + \lambda t)$ $E_J(H, H) = [(F - a)/2 - C]/(1 + \lambda t)$	$E_F(H, D) = F$ $E_J(H, D) = 0$
	DOVE	$E_F(D, H) = a$ $E_J(D, H) = (F - a)$	$E_F(D, D) = (F + a)/2$ $E_J(D, D) = (F - a)/2$

Figure 5: Payoff matrix of the hawk-dove foraging game, where  $F$  is the total number of items contained in the food clump,  $C$  is the energetic cost induced by fighting,  $a$  is the finder's advantage,  $\lambda$  is the encounter rate with food clumps, and  $t$  is the mean contest duration. (Dubois et. al, 2003)

\*\*note that in this matrix,  $E_F$  denotes the payoff to the finder and the finder's strategy is indicated by the first letter in the parentheses ( $H, H$ ) while the joiner's strategy is indicated by the second letter.

This payoff matrix was also used for the initial further exploration of the Dubois et. al model and all equations were kept the same.

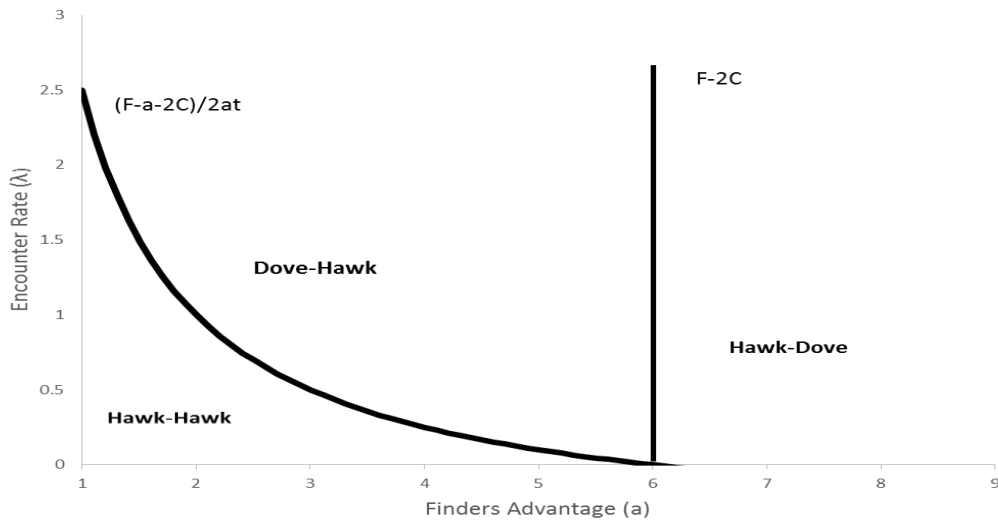
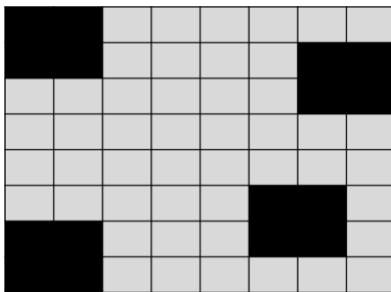
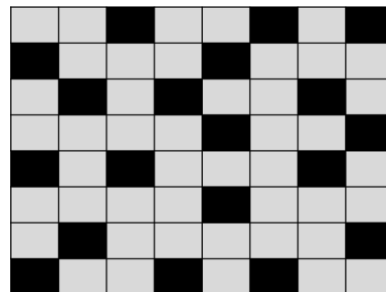


Figure 6: The evolutionarily stable strategy in relation to the encounter rate with food clumps and the finder's advantage.  $F=10$ ,  $C=2$ ,  $t=1$ . (reproduced from Dubois et. al, 2003). When the finder's advantage is low, but so is the encounter rate, it pays for both individuals to be a hawk in this model. The results of this model, however, do not simulate the effects of changes in the size of the food patch ( $F$ ).



Hypothetical chimpanzee-like world

Relatively high rates of aggression in a world with:  
 High  $F$  (food clump size)  
 Low  $\lambda$  (encounter rate)



Hypothetical gorilla-like world

Relatively low rates of aggression in a world with:  
 Low  $F$  (food clump size)  
 High  $\lambda$  (encounter rate)

Figure 7: Hypothetical representations of the model world that we sought to simulate by manipulating the variables of Dubois *et. al*. Black squares represent food clumps, while gray squares represent empty space. In the model gorilla world there are high numbers of food patches that are widely dispersed, but are small and low quality. In the model chimpanzee world, food clumps are high quality and large, but are spatially scarce. These environmental conditions have been hypothesized as one of the main ecological differences in the great apes and have been linked to the social characteristics of each species.

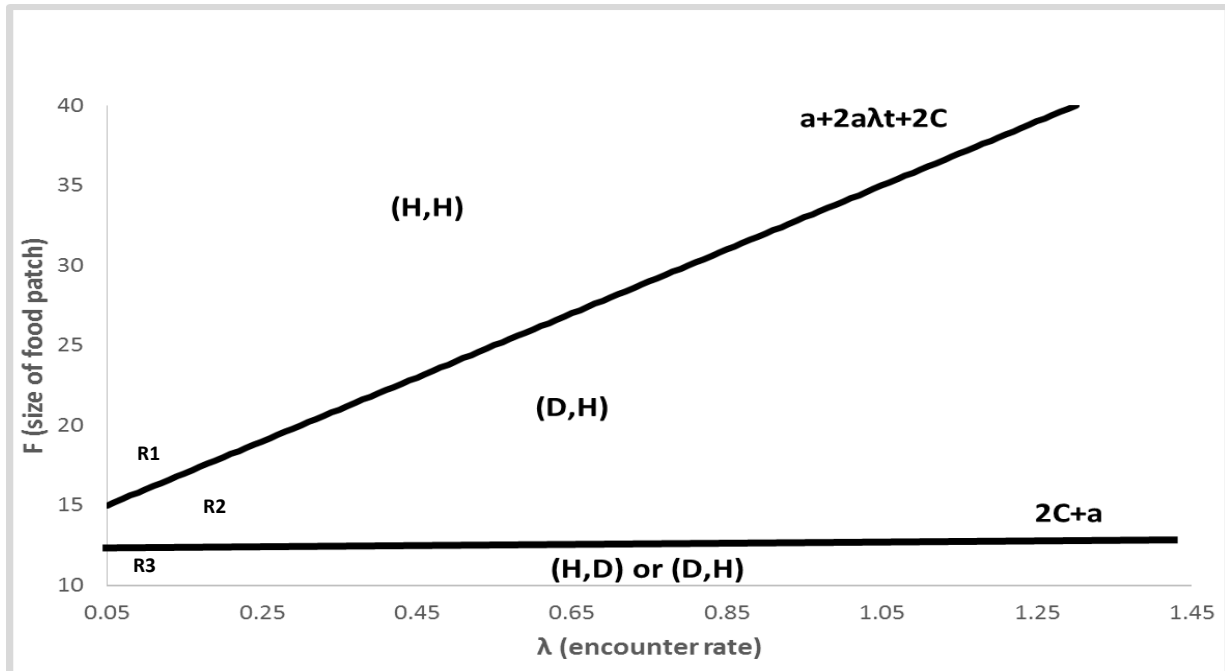


Figure 8: Evolutionarily stable strategies of chimpanzee and gorilla-like individuals in varying ecological conditions where food quality/size of food clumps ( $F$ ) and dispersal/encounter rate of food items ( $\lambda$ ) change.  $C=2$ ,  $t=1$ ,  $a=10$ . Note that the strategies of initial individuals change at the threshold  $F=a+2a\lambda t+2C$  and strategies of opposing individuals change at the threshold  $F=2C+a$ . Regions of the figure are represented by “R1” etc. In R3, there are two potential ESS’s that individuals can have.

		Choice of the Joiner	
		HAWK	DOVE
Choice of the Finder	HAWK	$E_F(H, H) = [(F + a)/2 - C]/(1 + \lambda t)$ $E_J(H, H) = [(F - a)/2 - C]/(1 + \lambda t)$	$E_F(H, D) = F - z$ $E_J(H, D) = 0$
	DOVE	$E_F(D, H) = a$ $E_J(D, H) = (F - a) - z$	$E_F(D, D) = (F + a)/2$ $E_J(D, D) = (F - a)/2$

Figure 9: Expanded payoff matrix of the choices of two individuals meeting in a hypothetical great ape-like environment. The base equations have been kept the same as in the Dubois *et. al* model, however the cost of chasing another individual “ $z$ ” has been added to this new matrix. This cost only applies when a Hawk and Dove meet. All other variable and parameter definitions are kept the same.  $C=2$ ,  $t=1$ ,  $a=10$ ,  $z=0.2$ .

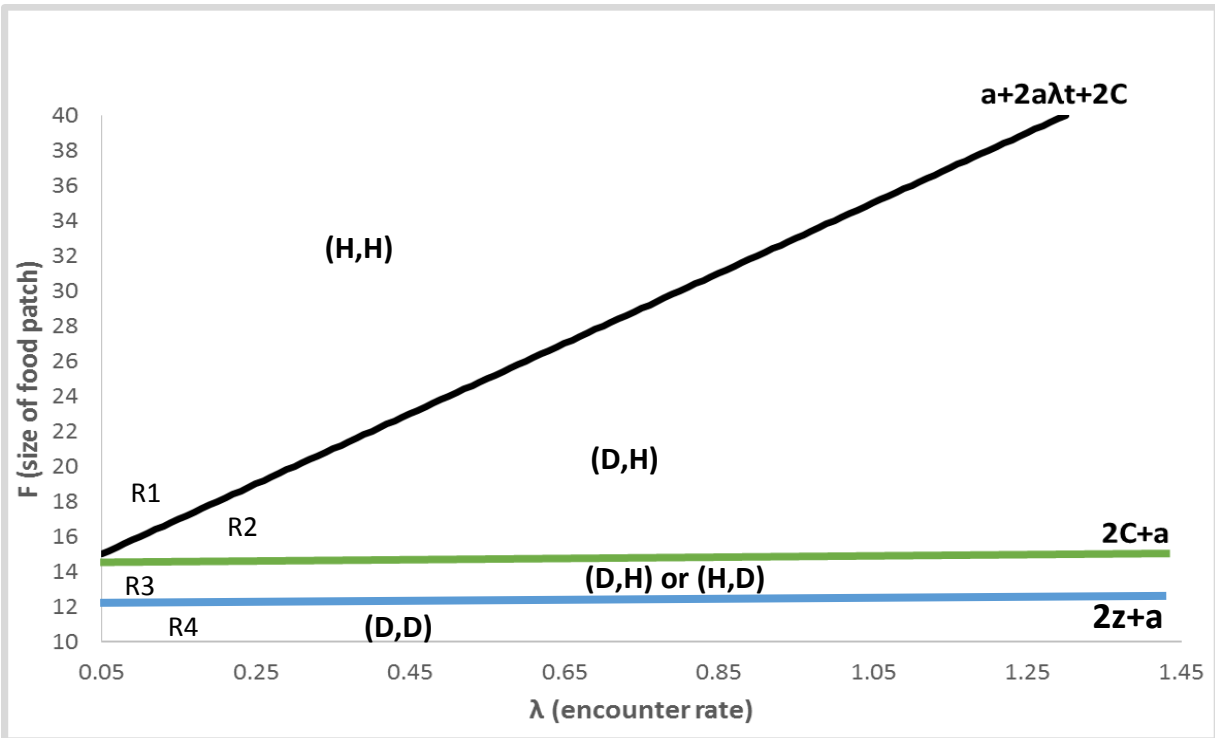


Figure 10: Evolutionarily stable strategies of hawk (chimpanzee-like) and dove (gorilla-like) individuals in varying environmental conditions. Note that Regions 1, 2, and 3 of this figure are consistent with those in Figure 8, however the cost of chasing off an opponent “z” has been included here, leading to Region 4 in this figure. Here (D,D) behavior emerges in environments with extremely low quality of food when there is a cost to a hawk chasing off a dove opponent.  $C=2$ ,  $t=1$ ,  $a=10$ ,  $z=0.2$ .

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