

Habitat and Dietary Differences between *Gorilla gorilla gorilla*
and *Gorilla gorilla beringei*: Implication for Social Variability

by

Jacklyn C. Bate

B.G.S., Simon Fraser University, 1985
B.A. Malaspina University College 2001

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

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in

THE FACULTY OF GRADUATE STUDIES

DEPARTMENT OF ANTHROPOLOGY
And SOCIOLOGY

We accept this thesis as conforming
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Abstract

In this thesis I examine and synthesize the research literature on the habitats, diets and behaviors of *Gorilla gorilla beringei* (mountain gorilla) and *Gorilla gorilla gorilla* (western lowland gorilla). Sympatric chimpanzees and the eastern lowland gorilla habitat, diet and behaviors are introduced when they elaborate significant aspects of *Gorilla gorilla beringei* or *Gorilla gorilla gorilla*. The contrasting habitats, diets, ecological adaptations and behavioral consequences among the gorilla subspecies are rationalized in relation to Wrangham's 1980 ecological model and the socio-ecological model, e.g., of 1997 as stated by Sterck and co researchers. Habitat, dietary and behavioral differences between the western lowland gorilla and the mountain gorilla calls into question the use of the mountain gorilla social system as a norm for all gorilla subspecies. However, problems in contrasting and examining the differences among the subspecies is heightened by a lack of long term behavioral studies on the western lowland gorilla, the numerically largest subspecies. Lack of habituation, visibility and tracking in aquatic herbal feeding sites have hindered behavioral studies of *Gorilla gorilla gorilla*. Significant issues are raised in relation to the risk of infanticide as a primary mechanism for female gregariousness across all gorilla subspecies. Moreover, the gorilla (primate) social system as delineated by Keppeler and van Schaik in 2002 demonstrates that other important areas of sociality (e.g., group cohesiveness) differ among the subspecies. Additionally, annotations of selected literature that apply to the subspecies' ecological issues (i.e., dietary and habitat particulars) with emphasis on the western lowland gorilla are presented as a baseline of ecological comparisons and research balance. Within the present data, although sociality and behaviors differ among the gorilla subspecies, the primary behavioral characteristics (e.g., female and male natal group dispersal) of each social system are similar. The caveat is the need for behavior studies of western lowland gorilla that are based on direct observation and not primarily indirect observation. Without such research the theory and behavioral characteristics of the mountain gorilla become the social system and theoretical basis of the western lowland gorilla despite the habitat, dietary and behavioral variations across the gorilla subspecies.

Table of Contents

| | |
|---|-----|
| Abstract | ii |
| Table of Contents | iii |
| Chapter I: Introduction | 1 |
| Theoretical Background | 2 |
| The Mountain Gorilla: Habitat and Diet | 4 |
| The Mountain Gorilla: Behavioral Particulars and Social System | 8 |
| Chapter II: Western Lowland Gorilla Research: Lack of Habituation and Visibility, the Results | 16 |
| Chapter III: Western Lowland Gorilla: Habitat, Diet, Behavioral Particulars and Social System | 23 |
| Western Lowland Gorilla: Habitat and Diet | 23 |
| Western Lowland Gorilla: Behavioral Particulars and Social System | 29 |
| Chapter IV: Discussion | 37 |
| References Cited | 43 |
| Appendix A: Selected Annotated Bibliography on Flora and Some Fauna Species Present with Particular <i>Gorilla gorilla</i> Sites in Relation to <i>Gorilla gorilla</i> Diet and Ecology | 48 |
| Introduction | 49 |
| Mountain Gorilla | 50 |
| Western Lowland Gorilla | 52 |
| Eastern Lowland Gorilla | 61 |
| Miscellaneous | 62 |
| Brief Discussion on Selected Annotated Bibliography | 62 |

Habitat and Dietary Differences between *Gorilla gorilla gorilla* and *Gorilla gorilla beringei*: Implications for Social Variability

Over evolutionary time, it is likely that a species foraging niche, social behavior and possibly non-foraging benefits of sociality will coevolve to produce the direct levels of food competition, group size and social structure we see today. Thus it should be useful to understand how food competition in a population depends on kinds, abundance and spatial distribution of resources used. This knowledge could be combined with known or estimated diets to predict group size and social systems. Such an analysis will be incomplete without understanding the social mechanisms by which individuals of a given species avoid predation or acquire other non-foraging benefits (Janson and Goldsmith 1995, p. 335).

Chapter I: Introduction

The habitat and diet of the mountain gorilla (*Gorilla gorilla beringei*) differ from those of the western lowland gorilla (*Gorilla gorilla gorilla*) (Doran, *et al.* 2002; Doran and McNeilage 1998, 2001; Goldsmith 1999b; Magliocca and Gautier-Hion 2002; Marchant 1996; Parnell 2002; Stokes *et al.* 2003; Taylor 2002; Tutin 1996; Watts 1996; Yamagiwa *et al.* 2003; Yamagiwa, *et al.* 1996). Diet and habitat diversity raises questions about possible variation in social systems between the two subspecies (*sensu* Eisenberg, *et al.* 1972; Dunbar 1989; Sterck, *et al.* 1997; Wrangham 1979, 1980). In this study I examine and synthesize the literature on the habitats and diets of the western lowland gorilla (WLG) and mountain gorilla (MG). The eastern lowland gorilla's (ELG) habitat, diet and social behaviors are introduced only when they elaborate significant aspects of diet, habitat or behavioral differentiation between *Gorilla gorilla gorilla* and *Gorilla gorilla beringei*. Furthermore, I consider and summarize the literature on possible disparities in the social systems between the WLG and MG as the variations relate to habitat and diet differentiation and the consequences of the variabilities to our understanding of the genus, *Gorilla*. Finally, two specific topics on WLG cited research data are evaluated.

Data gathered on the social system of the genus *Gorilla* have been the result of extensive behavioral research on MG communities (Doran and McNeilage 2001; Stokes, *et al.* 2003; Watts, 1996; Yamagiwa, *et al.*, 2003) in the highland regions of the Virunga Volcanoes (e.g., Fossey 1983; Schaller 1963; Watts 1994, 1995, 1996, 2000a, 2000b) or at Bwindi Impenetrable National Park, Uganda (e.g., Schaller 1988 [1964]; Stanford and Nkurunungi 2003). However, *Gorilla*

gorilla beringei is the least copious of the three subspecies (Stewart *et al.* 2001), and as noted by Schaller (1963), are habitués of an ecologically extreme area, i.e., ranges over 4000 meters higher than other gorilla habitats. The altitude, hence climate and soil conditions, have consequences for forest type and other vegetation variation (Tutin 1996; Tutin and White 1999; Watts 1996). What are the particulars of the habitat variables and what, if any, are the consequential social system differences between the WLG and the MG? In the first chapter I discuss the theoretical background of the posed question and review the pertinent literature on the habitat, diet and social system of the MG.

THEORETICAL BACKGROUND

In the effort to seek an evolutionary account for the extensive social diversity among nonhuman primate species, and at times populations, the influence of ecological factors on social systems was assessed. Trivers (1972) and Emlen and Oring (1977) demonstrated that although access to females is a primary fitness strategy for males, access to food is a priority for females, i.e., food resources limit female fitness and access to females limits male fitness (see Moore 1984 for review and analysis of inclusive fitness). Since food supplies are a determining variable for female reproductive success, the quality, distribution and density of food resources are primary in shaping the temporal and spatial distribution of females. (Wrangham 1979, 1980). The role and abundance of food, then, create social strategies, which in turn influence social systems (see Lee 1994).

According to Wrangham (1980) when food resources are evenly distributed and abundant, a scramble competition for food occurs. Female relationships are without a clear dominance hierarchy. Conversely, if food distribution occurs in patches, e.g., as with fruit trees, then a contest for food exists. With contest competition female relationships are "bonded", dominance patterns emerge and the females are philopatric (also see Watts 1994). Furthermore, a contest relationship exists between conspecifics and polyspecifics. However, the focus of

Wrangham's (1980) ecological model was the primate female and female-to-female relationships (Strum and Fedigan 1999).

Wrangham's model was expanded. Female to male associations were researched with regard to the primate females' need for predation protection to maximize her fitness (e.g., see Anderson 1986; van Schaik 1983; Isbell 1991,1994; Janson and Goldsmith 1995) and her strategies to counter infanticide by outside males (Harcourt and Greenberg 2001; van Schaik 1989, 1996; van Schaik *et al.* 1999; Sterck *et al.*1997). Sterck's, Watts' and van Schaik's (1997) socio-ecological perspective suggests that female gregariousness was determined by an interaction among food distribution, predation and infanticide pressures (*sensu* Hrdy 1979). According to van Schaik (1989, 1996) females have evolved counter-strategies to the risk of infanticide from non-community males. Embedded in the socio-ecological model is female choice of a male protector (see Stokes *et al.* 2003; Yamagiwa *et al.* 2003). Female gorilla group transfer, then, may be based on the quality of a male (Stewart and Harcourt 1987) and not exclusively on feeding competition as argued by Wrangham (1980).

Although the socio-ecology model acknowledged and analyzed an increased number and type of variables influencing female gregariousness, I suggest that environmental pressure, i.e., food distribution, remains basic (see Blake and Fay 1997; Janson and Chapman 1999; Janson and van Schaik 1988; Keppeler and van Schaik 2002; Koenig 2001). Logically, the socio-ecological view maintains that the ecological model is necessary, but is not sufficient. Furthermore, Goldsmith (1999a) argues that diet influences foraging efforts and variation in spatial/temporal relationships linked to day range length. Day path length is important to the species' type of social system (Janson and Goldsmith 1995; Terbough and Janson 1986).

The socio-ecological perspective models primate social behavior in terms of individuals maximizing biological processes, i.e., reproductive success, and social systems are the outcome of the interaction of primate reproductive strategies, predation, diet and food distribution (Janson 1992; Strum and Fedigan 1999). However, the individually created social organizations in

themselves generate behavioral parameters on the individual, i.e., the outcome is a feedback loop that is often quite complex (Keppeler and van Schaik 2002; also see Keppeler 2001) and ultimately involves conspecific and polyspecific inter-group relationships as well as intra-group behaviors. Where appropriate within this thesis I will note certain implications of the embedded Wrangham hypothesis (1980) as well as elements of the socio-ecological model (Sterck *et al.* 1997).

The concept of “social system”, however, can be unclear. As Keppeler and van Schaik (2002) note, social systems “focus on the traits of groups and not on individuals”(p. 708). The discussion of social systems in this thesis is best facilitated and explicated by use of Keppeler and van Schaik’s delineation of the ‘social system’ as three interacting components, i.e., social organization, social structure and mating system. Social organization is comprised of group size, sex composition and spatial-time relationships (also Kappeler 2001; Janson and Goldsmith 1995). Social structure refers to the patterns of social interaction and the resulting relationships (e.g., female-female, male-female, male-male, infant male-alpha male) (also see Janson 1988). The mating system within the genus, *Gorilla*, is considered a combined defense and sequential/polygynous pattern (Sterck *et al.* 1997; Watts 2000a). As discussed later, how this pattern is or is not maintained is a consideration in *Gorilla gorilla* subspecies’ social system variability.

THE MOUNTAIN GORILLA: HABITAT AND DIET

At the adjoining borders of Rwanda, the Democratic Republic of the Congo and Uganda, the Virunga volcanic region crosses seventy-seven miles of the Albertine Rift. Within Uganda is the Bwindi Impenetrable Forest National Park. These expanses are habitats for the two populations of *Gorilla gorilla beringei*. Amid the Virunga peaks (with intervening saddles or meadow areas) the MGs range between 2200 m to 4500 m. in altitude (Doran and McNeilage 2002; Emlen, Jr. and Schaller 1963; Schaller 1963; Stewart *et al.* 2001). Succinctly, the Virunga

area is designated as montane forest with blanketing terrestrial herbaceous vegetation (THV) (Schaller 1963; Fossey 1983; Stewart *et al.* 2001; Watts 1996). The MGs' Bwindi range extends to altitudes of 2200 to 2300 meters, i.e., comparable to the lower sections of that of the Virunga habitats. The forests are heterogeneous (total of 163 tree species with a small bamboo zone of the total area, 2%, compared to 50% in the Virunga region [Stanford and Nkurunungi 2003]). THV in the Bwindi gorilla habitat also tends to have extensive blanket-type distribution (Schaller and Emlen, Jr. 1963; Stanford and Nkurunungi 2003, see Appendix A). Foraging is ninety percent terrestrial (Watts 1996). Furthermore, MGs rarely build nests above ground, i.e., about ninety-seven percent are terrestrial (Watts 1995).

The perception of a blanketed Virunga region by THV carries a caveat. McNeillage (2001), for example, emphasizes a variation in terrain, vegetation (type and density) and a differentiation in frequency of foraging use. Areas between 2800-3300 m (sides of the volcanoes) have open dense herbaceous vegetation (74.94 g/m² food density). This type of vegetation constitutes 47.8% of the mean daily feeding sites of McNeillage's studied gorilla group I (named BM). Gorilla group II favored *Memulopsis* sites (open herbaceous areas located in a flat saddle) at 2500 to 2800 meters. Despite a considerably lower food density (20.08 g/m²) in relation to the higher foraging area of Group BM, Group II had a mean daily attendance for foraging in this area of 80.7 %. Both favored feeding sites constituted the largest type of terrain/coverage within the home range (group BM, 68% and Group II, 80.7%) (McNeillage 2001). The relationship between degree of density and foraging site may be mitigated by lesser energy costs when sequential food is evident (see Dunbar 1989). At the high altitudes fruit is unavailable; hence, the THV diet supplies energy and protein needs to the large gorilla body (Tutin and Fernandez 1993; Watts 1996, 2000b; also see Dominy *et al.* 2001 for summary of sensory protein detection; Plumtre 1995 on chemical composition of montane forests and effects on animals).

Moreover, at high foraging altitudes THV is supplemented with bark, grubs, termites, dirt and dung (Fossey 1983, also see Appendix A). Fossey notes observations of coprophagy as practiced by both gorilla sexes of all but the unweaned, usually after extensive rests during the rainy season. The benefits may include an ability of vitamins (especially vitamin B₁₂) to be assimilated in the foregut and ingestion and the absorption of nutrients not available in plant matter (Fossey 1983). Consuming potassium and calcium rich dirt occurs in binges during the dry months (Fossey 1983; Watts 1996; in contrast see Magliocca and Gautier-Hion 2002 on potassium, calcium and sodium dietary enrichment for WLG; also refer to Magliocca and Gautier-Hion 2002 in Appendix A).

The MG, then, is classified as a folivore (Doran and McNeilage 2001; Fossey 1983; Remis 1997b, 2000; Remis *et al.*, 2001 [also Remis listings, Appendix A]; Schaller and Emlen, Jr., 1963; Watts 1996). Less than one percent of the Virunga MG diet contains fruit (Watts 2000b [see Appendix A]; Yamagiwa *et al.* 2003). According to Taylor (2002) in comparison to those in the WLG, the MG's mandibular corpus and symphysis are wider, a possible result of a more resistant diet. Although anatomical evidence is limited (Remis 2000), gorillas appear anatomically equipped to digest fiber (Hladik *et al.* 2002; Taylor 2002). The colon contains a large number of cellulose digesting ciliate. Furthermore, there is sufficient length of gastrointestinal food retention to permit a large hindgut termination capacity (Remis *et al.* 2001; Watts 1996). However, unlike the folivorous colobines, gorillas are not morphologically specialized to detoxify alkaloids with forestomach fermentation (Oates *et al.* 1977; Remis 2000; also see Dominy *et al.* 2001 for summary of toxin detection). Hladik *et al.* (2002), Remis (2000) and Taylor (2002) analyses indicate that the morphological/ physiological digestive system of the gorilla is consistent with a diet that contains fruit.

Janson-Seaman and Kidd (2001) note that MitochondriaDNA studies demonstrate no difference between the Virunga and Bwindi gorilla populations. Remis (2000) suggests that during evolutionary diversification, increased body size of highly frugivorous ancestors helped

create dietary flexibility. The flexibility permitted retreat into high altitudes where fruit is scarce (Groves 1986; Remis 2000; Yamagiwa *et al.* 1996, further detail refer to Appendix A). Stanford and Nkurunungi's (2003) data support a significant difference between the Bwindi and high altitude MG habitats in availability of fruit and gorilla dietary patterns. Unlike the Virunga habitat, the Bwindi area produces ripe fruit each month although the number of ripe species and amount of fruit varies. Both sympatric chimpanzees and the MGs include such fruit in their diets. While the Bwindi MGs rely on THV as a fallback or lean staple food as well as an overall source of protein, they spend approximately 50% of their daily eating time consuming fruit of various species (Stanford and Nkurunungi 2003).

Overall, then, the classification of the gorilla as a folivore appears to emanate not only from one subspecies, i.e., the MG, but also only from the high altitude portion of that subspecies, i.e., *Gorilla gorilla beringei* of the Virunga region above 2800 m. At lower elevations the Virunga MGs eat more fruit and generally have a more varied diet than do their counterparts at higher elevations (McNeilage 2001; Goldsmith 1999b). However, according to Yamagiwa *et al.* (1996) the ELGs who inhabit highland tropical forests show a dietary composition similar to the highland MG although the authors' acknowledge that the ELGs' diet includes a wider variety of flora species than highland gorillas. In my review of Yamagiwa *et al.* data (as published, 1996) I found the comparison somewhat generalized. First, as stated, the designated ELG highland areas contain fruit (which is eaten) and a larger diversity of consumed flora species than present in the Virunga Volcano high altitude MG. Second, although the ELG habitat may extend to 3300 m in altitude, the lower elevations (to 1800 m) appear as a significant part of the gorilla range. These designated ELG lowlands also have extensive fruit usage and a food diversity which exceeds that of even the low altitude MG (Watts 1996; Yamagiwa *et al.* 2003). Therefore, it is doubtful that the ELG's habitat and dietary consumption are robustly comparable to MGs' habitat and dietary consumption.

Within the three subspecies, then, the high altitude populations of the MG have the most restricted diet (Doran *et al.* 2002; Doran and McNeilage 2001; Jones and Sabater Pi 1971; McNeilage 2001; Magliocca and Gautier-Hion 2002; Remis 1997a, 2000; Taylor 2002; Watts 1996). Furthermore, although the Virunga Volcano region comprises one continuous ecosystem (see overview in McNeilage 2001 and/or Stewart *et al.* 2001), it is also a complex region with variations in altitude and flora that produce diverse smaller enclaves within the generalized montane habitat. About three hundred *Gorilla gorilla beringei* range the volcanic highlands. The remaining two hundred to two hundred and fifty of this subspecies habituate lower altitudes of the Virunga Volcano Park or the Bwindi region of Uganda (see Doran and McNeilage 1998, 2001 for summary of subspecies population figures). However, the Virunga Volcano MG population is the best studied because the Karisoke Research Center (Rwanda), founded by Dian Fossey, (see Fossey 1983) has achieved three decades of research on *Gorilla gorilla beringei*'s habitat, ecology and behavior of habituated gorillas.

MOUNTAIN GORILLA: BEHAVIORAL PARTICULARS AND SOCIAL SYSTEM

The Virunga Volcanic region may be viewed as the "classic home" of MGs (Stewart *et al.* 2001). The densely and evenly-distributed THV of the region meet the criteria of Wrangham's (1980) ecological model of food distribution in relation to the non-bonded, non-hierarchical female-female relationships. *Gorilla gorilla beringei* exhibits this category of female-female relationship (Fossey 1983; Schaller 1963; Tutin and White 1999; Watts 1994; and see Wrangham 1980). Furthermore, characteristic of gorilla social structure (*sensu* Keppeler and van Schaik 2002) is female voluntary transfer from their natal group before reproductive maturity as well as somewhat frequent secondary transfers (Fossey 1983; Schaller 1963; Stewart and Harcourt 1987; Watts 1996; Yamagiwa *et al.* 2003). For example, Watts' (1996) data on twenty-nine mature MG females established that twenty-two of the studied females transferred groups one to four times (also see Fossey 1983; Stewart and Harcourt 1987 for further data analysis). However, it should

be noted that the study by Watts (1996) shows the female dispersal pattern from the natal group to be common, but not universal. Only a few primates, for example, Thomas langurs (Sterck and Steenbeck 1997) or the hamadryas baboons (Moore 1984) share a similar female dispersal system and food distribution pattern (also see Sterck *et al.* 1997; Stokes *et al.* 2003; Watts 1996). Yet simply noting female dispersal activity leaves the question as asked by Palombit (1999): Why do adult gorilla male-female bonds exist beyond estrus?

Sterck *et al.* (1997), van Schaik (1996), van Schaik *et al.* (1999) and Watts (1996, 2000a, 2000b) propose that a primary mechanism of the mountain gorilla social structure is the male gorilla's adaptive fitness strategy, i.e., acts of infanticide (*sensu* Hrdy 1979; also see van Schaik *et al.* 1999 for physiological particulars). MG adult males can and do kill unrelated unweaned infants (Sicotte 1993; van Schaik 1983, 1996; Watts 1989, 1996, 2000a; Yamagiwa *et al.* 2003). Counter strategies are evident in adult female MGs, i.e., they associate with the putative father of the infant not only for copulation during estrus, but also for protection from infanticide risk by outside-group adult males (Fossey 1983; Goldsmith 1999b; Harcourt and Greenberg 2001; also see Doran and McNeilage 2001). Generally, gorilla sexual dimorphism makes it difficult (if not impossible) for adequate female physical defense against infanticide (Watts 1996).

Watts (1992, 1994, 1995, 1996) concludes that adult female MGs spend more time close to males than to other females within the group (also see Stewart and Harcourt 1987). Significantly, females with infants remain spatially closer to a group male (and will do so aggressively if necessary) than those females without unweaned infants (Watts 1992). Although females are free to transfer groups as they so choose, MG females with unweaned infants do not transfer (Watts 1989; also see Stokes *et al.* 2003). Episodic observations and life history records at Karisoke Research Center reveal incidents of infanticide when female gorillas have transferred groups with a young infant after the death of a silverback (Fossey 1983; Watts 2000a).

Similarly, upon review of Karisoke research data, Doran and McNeilage (1998) conclude that female emigration and immigration are not primarily related to ecological factors, i.e., such

decisions are independent of competition for food (summary in Stokes *et al.* 2003; Yamagiwa *et al.* 2003). Doran and McNeilage's (1998) perspective, data and analysis embraces Sterck *et al.*'s (1997) socio-ecological model and its emphasis on female emigration and immigration based on the silverback quality for protection from infanticide and predation (Yamagiwa *et al.* 2003; Watts 2000b). Additionally, according to Watts (2000a) home range overlap, low variation in home range food quality and variety reduce the importance of familiarity of natal areas for female foraging efficiency, thereby negating a correlation between transfer and food resources as a primary consideration.

Of importance to the issue of female dispersal is Watts' (1996) conclusion that group size is not an influence on female transfer decisions. Accordingly, female gorillas do not transfer to smaller groups where there would be less food competition; again, greater resource acquisition is not a key factor for emigration. Moreover, ecological and social costs for female gorillas who transfer are minimal. Watts also finds that the female counter-strategy to infanticide risk (seeking silverback protection) is a crucial influence on the decision to change groups while the judged quality of the leading male and the subsequent ability of the group organization to offer protection determines the ultimate decision (Sterck *et al.* 1997; Watts 1994, 1996, 2000b). According to Doran and McNeilage (2001) the average MG female experiences infanticide at least once in her lifetime; therefore protection from infanticide risk is essential to female reproductive strategy. The importance of male leadership quality and infanticide protection, then, are viable explanations of new group selection by adult MG females.

Van Schaik (1996) offers a word of caution on the underlying fitness perspective within the socio-ecological model. Van Schaik warns that the ecological impact on female spatial association and the direct male response to that association are oversimplified. For van Schaik the actuality of significant male-female social relationships generates a complexity that alters the strictly ecological precept on social organization and social structure (also see Sterck *et al.* 1997; Watts 1996). The cohesiveness of MG social organization is predicated on long-term male-female

social bonds, i.e., adult gorillas' life histories include membership in groups that are lead by an adult male who is the main mating partner for the group's females (Harcourt and Greenberg 2001; Stewart and Harcourt 1987; Watts 1995). Within the reproductive group, the bond of each female to the silverback leader creates a pervasive influence of sociality, e.g., in group movement which reflects not only group organization (spatial-time relationships), but also cooperative cohesion (see Boinski and Garber 2000). It is evident, then, that evolutionary causal factors for grouping are complex interactions of fitness mechanisms, a supportive ecology and feedback within the resulting social relations.

Adult female MGs do not travel alone (Schaller 1963; Fossey 1983). Emigration from natal groups by females is achieved during intergroup encounters (Stewart and Harcourt 1987; also see review, Doran and McNeilage 2001 who find transfer opportunities rare). Additionally, female MGs do not remain cohesive upon the death of the group's alpha silverback, but disperse to other groups or join lone male silverbacks (Fossey 1983; Stewart and Harcourt 1987; Watts 2000a).

However, within the Kuhuzi-Brega National Park (highland area at 1800m-3300m) of the Democratic Republic of the Congo, a different pattern emerges from the ELG groups. Yamagiwa *et al.* (2003) states that after the death of the group's silverback leader, the females of the group may remain cohesive, i.e., continue to associate and travel together for up to twenty-nine months without a male leader. Extra-group silverbacks may visit from time to time during the "leaderless period" (Yamagiwa *et al.* 2003). Noted also is an absence of infanticide by ELG adult males (no observed infanticide and life history records available on the adult females and their offspring indicate no infanticide) (Yamagiwa *et al.* 2003). This sharply contrasts with MG evidence where an unweaned infant arriving in a new group with its mother will rarely escape infanticide (Fossey 1983; Robbins 1995, 1999; Stewart and Harcourt 1987; Watts 1989). The global statement of infanticide risk within all gorilla subspecies, then, is simplistic and over-generalized. I found no

literature rationalizing this exception to infanticide risk within any model including the socioecological model.

Intra-group relationships between MG females are differentiated along kinship lines (Watts 1994, 1996) in that less aggressive behavior and more interactive association among related females are exhibited (Stewart and Harcourt 1987; Watts 1994, 1996). However, structurally, formal dominance relationships do not exist between adult MG females whose associations may be classified as dispersal-egalitarian (Sterck *et al.* 1997). Generally, then, agonistic events among adult MG females remain unresolved, lack a linear dominance hierarchy, have little importance to female fitness (thereby have no effect on the mating system [*sensu* Keppeler and van Schaik 2002]) and are not ascribed to resource competition (Watts 1992, 1994, 1996). Furthermore, positive interactive gregariousness among adult female MGs through mutual grooming is minimal although females do groom younger animals in the group and especially their own infants (Fossey 1983; Emlen, Jr. and Schaller 1963; Schaller 1963; Schaller 1988 [1964]).

As well as adult females, maturing MG males emigrate from their natal groups (Fossey 1983; Goldsmith 1999b; van Schaik 1996; Watts 2000a, 2000b) although Robbins (1995) finds that only thirty-six percent do transfer (see Yamagiwa *et al.* 2003 for summary of habituated ELG male transfers since 1977). Schaller's (1963) observation that WLG groups may have more than one mature male is consistently supported by primatological research (review: Yamagiwa *et al.* 2003). However, the MG groups have significantly higher percentages of multi-male (silverback) groups in relation to ELG or WLG (Yamagiwa *et al.* 2003). Despite the possibility and actuality of multi-male gorilla groups, a defining characteristic of gorilla social organization is that only one male (silverback) per group has control and leadership (Fossey 1983; Robbins 1995; Schaller 1963; Watts 1996).

At maturity a male gorilla has three general options. He may leave the group and become either a solitary male or part of an all male group, or he may remain subordinate to the alpha

silverback in his natal group (Doran and McNeilage 1998, 2001). A pattern of age-graded male social structure may emerge (*sensu* Eisenberg *et al.* 1972; also see Robbins 1995, 1999, 2001) although those males who are kin to an alpha male (e.g., a son) are more easily tolerated by the lead silverback if the choice is to remain with the natal group.

Doran and McNeilage (1998) suggest that those who remain in the natal groups are somewhat more successful at gaining access to females than do those who become lone males (also see Yamagiwa *et al.* 2003 on lack of any observation of male take-over of a group by extra-group silverbacks). Subordinate adult male gorillas in a group may become an adult female's social partner or he may copulate with her (Robbins 1995, 2001). Subordinate males may also groom infants (Sicotte 1994). Because females transfer groups, alpha silverbacks compete to attract them to their group (Sicotte 1993, 1994). Although speculative, it is argued that tolerance of other adult males by the lead silverback occurs to entice females to join and to remain with the group. Such a possibility is a social variant consistent with the fitness hypothesis of male social dispersion (see Mitani *et al.* 1996 for a cross species analysis).

Upon reaching maturity, then, the silverback male may be solitary, be a subordinate follower in the natal group, build his own group, join an all-male group, take over an existing group (usually upon the death of the reigning silverback) or transfer among these options (Doran and McNeilage 2001; Fossey 1983; Schaller 1963; Sicotte 1993; Watts 2000a). Within the life history of the adult male MG, transferring among options is common (Doran and McNeilage 2001; Watts 2000a). Although van Schaik's concern (1996) stated above, i.e., concern of possible over-simplification inherent in the male fitness theory in relation to gorilla social organization, is acknowledged and accepted, the male fitness theory seems to hold within the data on male movements (dispersal) and the patterns of social interaction within gorilla social structure (see Robbins 2001; Watts 2000a).

Patterns of social interaction and the resulting relationships (female-female, female-male or male-male) partition the perspective of a primate species into behaviors representing the stated

category. The questions asked and the data gathered are limited to the inclusion of the interrelationships. For example, Watts' research perspective of 1992 and 2000a is the male-female relationship and its effect on group cohesion. However, in Watts' 2000b report on MG group cohesion the parameters of investigation take into account ecological factors. According to Watts (2000b) the dynamics of group cohesion include not only research on key relationships, but also data gathering and analysis on group size, day and home range and foraging strategies of MG groups. Hence, how the MGs use their habitat is significant in understanding their group organization.

Generally, the Virunga gorilla habitat is used to maximize foraging efficiency and day paths are short and feeding time in relation to a high dietary intake is short (Watts 1996). Moreover, the MGs forage in a cohesive unit and, unlike the chimpanzee, fission-fusion events are extraordinary (Doran and McNeilage 2001; Goldsmith 1996, Janson and Chapman 1999; Kuroda *et al.* 1996; Yamagiwa *et al.* 1996).

At any given time when foraging in the blanketed, dense THV of the Virunga habitat, the MG group may move only four to six meters between feedings (Watts 1991). The mean daily path length is short, i.e., 0.5 km. (Watts 1991; also Yamagiwa *et al.* 2003, Table 1 [p. 262]; contra Janson 1988). The annual home range averages (means) extends between 4 to 11 km² (Doran *et al.* 2002). According to Watts (2000b) only small portions of annual home ranges are used most of the time. However, extreme male-male mating competition can be a primary influence on group movement and create range shifts (Watts 1994). Ecologically, bamboo shoots, a preferred and seasonal food in the MG diet, may alter group pace and distance. Using vocalizations to control movement, a MG group may travel up to a kilometer in a state of great excitement from THV feeding area to bamboo forest (Watts 2000b). Both social (mating competition) and ecological (THV blanketing and preferred seasonal bamboo shoots) impact foraging strategies (Watts 2000a, 2000b; for 2000b refer to Appendix A).

Although mating pressures and bamboo preference, i.e., social and ecological considerations, are also factors for the Bwindi or lower altitude MGs, some Bwindi group particulars differ from the high altitude MG. The mean group size of the high altitude MGs is 9.15 (Watts 1996) while the Bwindi groups, although similar in mean size, exhibit a wider spread than the Virunga gorilla groups (review: Doran and McNeilage 2001). Yamagiwa *et al.*'s (2003) review found a greater food variety (including fruit) and longer day and annual ranges for the Bwindi gorillas in contrast to the Virunga gorilla groups. However, the close cohesiveness of the groups remained similar. The Stewart and Harcourt (1987) conclusion of the pervasive effect of the male-female bond (and lack of female bonding or hierarchy pattern) on gorilla cohesiveness was reasserted by Yamagiwa and colleagues (2003) (also see Watts 2000a; Stanford and Nkurunungi 2003).

Parker (1999) generalized that gorilla habitat, diet and foraging patterns express abundant evenly distributed food resources, small home ranges and cohesive groups. The compact foraging patterns allow each group's silverback to guard non-bonded females from competing males. However, although Parker's perspective does befit the high altitude MG, the data and patterns outlined above present habitat variation between the Virunga and Bwindi regions. Such variations are not expressed in Parker's perspective. In addition the Parker generalization excludes the strong social interactive variable in understanding and rationalizing MG group cohesiveness. Now the question is: How and to what degree do the data and inferences on the MG apply to the WLG? However, before the habitat, diet and social system of WLG are discussed, it is prudent to examine the problems of research with the wild WLG.

Chapter II: Western Lowland Gorilla Research: Lack of Habituation and Visibility; the Results

Unhabituated groups and dense forest undergrowth impede direct methods of research (e.g., data gathering via observation of events) in the THV habitats of the WLGs (Cipolletta 2003; Doran and McNeilage 2001; Magliocca *et al.* 1999; Parnell 2002; Stokes *et al.* 2003, Tutin 1996). Where aquatic herbal vegetation (AHV) attracts WLGs, tracking group movements, consistent researcher control over group selection and setting start or finish times for observations are not usually possible (Olejniczak 1994, 1997; Parnell 2002; Stokes *et al.* 2003; also see Altmann 1974 for review of *ad libitum* sampling). Therefore, in contrast with MG research results at Karisoke, little behavioral data on habituated WLGs and only limited published behavioral studies exist. Emphasis has been on ecological studies (Cipolletta 2003, Goldsmith 1999b; Parnell 2002; also see Doran and McNeilage 1998). In relation to research challenges, four categories of WLG research sites can presently be defined as follows:

1. In Gabon, Bai Hokou and Mondika locales, WLG habituation is on going, but incomplete. Information gathering can be episodic and/or indirect. Indirect research methods, i.e., use of fecal samples, trail signs and nest counts are used extensively to obtain WLG censuses (or WLG biomass densities), dietary particulars or foraging strategies (including daily path length) (Doran *et al.* 2002; Tutin 1996; Tutin and Fernandez 1984, 1993; Tutin *et al.* 1992). In the Central African Republic at Bai Hokou WLG studies are prepared based primarily on ecological monitoring and foraging patterns (including daily, monthly and annual ranges). As at Lope, Gabon, fecal analysis and trail signs provide the majority of the data base (Remis 1997a, 1997b, Remis *et al.* 2000).
2. At one research site at Lossi Forest in the north Congo region, WLGs are reportedly habituated for tourism. Data on group size and day range are available

as well as a pilot study for tourism, but no study on WLG group behavior or conspecific inter-relationships has been done (see Bermejo 1997, 1999a, 1999b).

3. At Mbeli Bai, Republic of Congo, observations of WLGs from a platform placed at the edge of a swamp have allowed gathering of demographic data, local dietary use, some episodic behavior and life history profiles. Maya Maya (Maya Nord), a saline clearing provides open observation, but is surrounded by dense forest with heavy undergrowth (Olejniczak 1994, 1996, 1997; Parnell and Buchanan-Smith 2001; Parnell 2002; Magliocca and Gautier-Hion 2002). The WLGs are habituated to the platform and its researchers (see Doran and McNeilage 2001; Magliocca *et al.* 1999; Olejniczak 1994, 1997). However, because of swampy terrain, the gorilla groups are not tracked (Doran and McNeilage 1998; Parnell 2002; Stokes *et al.* 2003).
4. In southeast Cameroon and Cross River regions (Nigeria) data gathering has been sporadic and indirect (see Doran and McNeilage 1998, Table I, p. 123). WLG diet, habitat analysis and census-taking have been primary goals (Deblauwe *et al.* 2003; Morgan *et al.* 2003). Additionally, information on the Cross River gorilla groups is part of a systemic reclassification debate on *Gorilla* (see Stewart *et al.*, 2001; also Jansen-Seaman 2001; Morgan *et al.* 2003).

In summary, Stokes *et al.* (2003) find that the lack of WLG habituation and the visibility impediment created by dense vegetation result in an emphasis on ecological studies and a dearth of information on WLG social organization or mating systems (*sensu* Keppeler and van Schaik 2002). The above categories support such a perspective. Furthermore, Parnell (2002) and Cipolletta (2003) argue that indirect data gathering can be problematic. Data gathered indirectly for census-taking, which may include age and sex delineation, dietary/nutritional or ranging pattern studies, for example, can lead to incorrect inferences and skewed comparisons among conspecific or polyspecific primate populations (Cipolletta 2003).

Within a given region, basic census-taking on WLGs is frequently based on nest counting without tracking or direct observation (e.g., Fay 1997; Mitani *et al.* 1993; Remis 1997b; Tutin and Fernandez 1984). Census-taking in areas where chimpanzees and gorilla home ranges overlap (e.g., Lope, Gabon), arboreal nests were assumed to belong to chimpanzees and were, therefore, not counted. However, it is presently known that 35% of WLG nests are arboreal (Magliocca *et al.* 1999). Furthermore, not all gorillas build nests each evening (Doran and McNeilage 2002; Bermejo 1997, 1999a, 1999b; Magliocca *et al.* 1999). It appears, therefore, that census figures may be inaccurate (likely underestimated).

Spatial-temporal relationships are closely related to social organization (*sensu* Kappeler and van Schaik 2002). Dietary habits and foraging strategies provide information on spatial-temporal relationships (*sensu* Wrangham 1980). Because the WLGs, compared to the MGs, consume more fruit, the WLGs also have a greater seasonal dietary variation than the MGs (Doran *et al.* 2002; Goldsmith 1999a; McNeilage 2001; Remis 1997a, 1997b; Remis *et al.* 2001; Stokes *et al.* 2003; Tutin and Lee 1999). Pacing daily WLG path lengths (e.g., Goldsmith 1999a), plotting daily map routes onto maps (e.g., Tutin 1996) or determining path lengths as mean averages from quadrates (set from line transit surveys; see Plumptre 2000) fails to include the effect of the variability and seasonality of the WLG diet (Cipolletta 2003; Yamagiwa *et al.* 2003). As discussed later, the implications of dietary variation on grouping and spatial/temporal behavior and intragroup relationships are significant for the WLG.

Doran *et al.* (2002) question the accuracy of fecal samples and trail sign data to determine the quantity of fruit consumption when the additional support of direct observation is excluded by lack of visibility or habituation (also see Magliocca *et al.* 1999). Doran and colleagues (2002) note that at Mondika, Central African Republic, data on dietary intake (which included AHV) showed no sex difference in quantity of intake. Doran and coworkers conclude that such results were due to indirect sampling, i.e., circumference measurements of feces to establish sex differences were not accurate. Such a method is compromised by differentiation in growth

patterns between male and female gorillas. The fecal circumference for an adult female is likely similar to the fecal circumference of a black-back male at a particular developmental stage. In addition, although fecal samples did indicate dietary intake diversity, the sampling method was a poor measure of amount of intake. Doran *et al.* (2002), Tutin (1996) and Goldsmith (1996) argue that trail signs used in dietary analysis do not permit sexual distinction nor do they measure how many individuals were present. Moreover, they may overestimate daily dietary variation (Doran *et al.* 2002).

Data on insectivory by WLGs in southeast Cameroon were gathered on unhabituated WLGs using indirect methods, i.e., fecal samples taken from trails and nest sites without observation (Deblauwe *et al.* 2003, see Appendix A, this thesis). Variety and individual frequency of insect species as part of the WLG diet were analyzed. Comparisons were made in reference to four other WLG research sites, i.e., Lope and Belinga, Gabon (e.g., Tutin and Fernandez 1992, 1993), Ndoki in the Congo (Kuroda *et al.* 1996) and Dzanga-Sangha, Central African Republic (Remis 1997b) (summary see Deblauwe *et al.* 2003, Table II, p. 498). As previously established, the degree of WLG habituation among these sites varies from none (Dzanga-Sangha) to partial (Lope). Deblauwe and colleagues (2003) used the same criteria to classify fecal samples as were used at the comparison sites. However, it is not the processing techniques or the statistical analysis (see Deblauwe *et al.* 2003, pp. 495, 497-498) that signal caution on inferences from the intersite dietary comparison. Concern over accurate results lies in the initial use of comparative data gathered by indirect methods and on gorilla groups in different stages of habituation. Lack of gorilla habituation and the challenges of these limitations to develop accurate gorilla research studies may be best clarified in examining daily path length research.

Examination of data determining the length of the WLGs' daily forage path demonstrates the degree of habituation (or not) is a significant variable in relation to the validity of indirect information gathering on basic ecological or behavioral questions about WLG issues (Cipolletta

2003; Parnell 2002; Tutin *et al.* 1991; Watts 2000b; Yamagiwa *et al.* 2003). Tutin *et al.* (1991) noted that unhabituated gorillas have a diverse response to researchers. Cipolletta's (2003) study correlated the habituation process to data on daily path length of a WLG group in Dzanga-Ndoki National Park, Central African Republic. Recorded reactions of fear (i.e., discontinuation of task, e.g., by fleeing or aggressive displays), acts of curiosity (which also halted the task-at-hand) or ignoring the researchers (initially a rare response) all contributed to altered usual path lengths. Ultimately, unhabituated alarmed gorillas alter, abandon or interrupt behavior. Cipolletta (2003) concluded the following:

1. As less fear and aggression were evident (plotted) the daily path lengths shortened from 2.3 to 1.6 km.
2. The monthly total of path lengths had no significant change due to a strategy of avoiding areas disturbed by unknown inhabitants, namely the researchers. Therefore, although the length did not change, the monthly pattern did.
3. Even when there was no direct contact between the gorillas and the researchers, the gorillas crossed trails with researchers and left indirect signs of alarm (e.g., see Remis 1997b).
4. Researchers not aided by trackers were more likely to record longer ranges than the gorilla group actually traveled (also see Tutin 1996).
5. Finally, it was also necessary to factor dietary influence (seasonality and location) into changes in path lengths (as well as the researchers' influence)(also see Doran *et al.* 2002) to obtain accurate daily path lengths.

Different levels of researcher disturbance, then, influence different levels of data. Furthermore, researcher contact with unhabituated gorillas has outcomes on a variety of activities that include not only daily path length, but also choice of immediate foraging site and actual dietary intake. With WLGs the seasonality and clumped location of food may also influence certain research outcomes.

Direct observational data are possible at saline research sites, for example, Mbeli Bai and Maya Nord (Stokes *et al.* 2003; Magliocca *et al.* 1999; Magliocca and Gautier-Hion 2002; Olejniczak 1994, 1997; Parnell 2002). In addition, it has been previously noted that where a platform is used for observations (Mbeli Bai), the gorillas are habituated to researchers on the platforms. However, because of a lack of tracking feasibility, with female transfer issues, for example, transfer dates lack accuracy (by a week to several months). Moreover, if a female simply does not reappear with her group the question arises if she transferred or if she died (Stokes *et al.* 2003). Other ecological research issues such as ranging, overall dietary and cost/benefit patterns require observation and tracking for completeness and robust accuracy.

Lack of visibility in forested areas, incomplete or no habituation and/or obstacles to tracking (or late tracking) of subject WLG groups, then, can influence research results on foraging strategies, accuracy in determining the role of combined patch (fruit and aquatic AHV) and dispersed (THV) food patterns in relation to group size, participant encounter rates and search field overlaps (*sensu* Chapman and Chapman 2000). In research projects where the dietary pattern and foraging strategies of the WLG are compared to those of the sympatric chimpanzee (e.g., Kuroda *et al.* 1996; Tutin *et al.* 1992), the comparison may be askew or problematic.

Moreover, when long term WLG behavioral studies are absent, the behavioral patterns of the MG may be assumed for the WLG (Doran and McNeilage 2001; Stewart *et al.* 2001; Yamagiwa *et al.* 2003). I suggest that when behavioral patterns of the MGs are assumed to be the behavioral patterns of the remaining two subspecies, the relationship of the socio-ecological model (e.g., Sterck *et al.* 1997) and the ecological paradigm (*sensu* Wrangham 1980) are also assumed to apply. For example, previously discussed is the lack of evidence to support infanticide risk within the ELG social system (see chapter one, pp. 11-12). Such variation questions the basic tenet (infanticide risk) of the socio-ecological model. However, when direct evidence of infanticide behavior is not available for the WLG, the socio-ecological model is used to support

infanticide risk as a pattern within the WLG social system (see Stokes *et al.* 2003; this issue is further discussed later in this thesis).

However, researchers over time have gathered information and data on the WLG within the strictures of environmental limitations and have worked to habituate WLG groups (e.g., Bermejo 1999a, 1999b; Cipolletta 2003; Doran *et al.* 2002; Jones and Sabater Pi 1971; Kuroda *et al.* 1996; Magliocca *et al.* 1999; Olejniczak 1994, 1997, 1999; Stokes *et al.* 2003; Tutin 1996). Olejniczak (1994, 1997) has used the innovative technique of a platform built at the edge of a swamp section at Mbeli Bai for direct observation of gorilla group activities. Cipolletta (2003) used the habituation process not only for data gathering on ecological events of the WLG study group, but also to better understand the limitations of data on, e.g., daily ranging activities, when the gorilla group was unhabituated or in process of being habituated (also see Tutin 1996). Bermejo (1997, 1999b) habituated a WLG group and has started behavioral observations as well as ecological and conservation data gathering. Chapter three of this thesis examines the habitats, diet and social system of the WLGs. Characteristics of these factors are compared to those of the MGs. Moreover, the diet, habitat and selected social characteristics of sympatric chimpanzees are compared to the WLGs when such a comparison elaborates our understanding of the WLGs.

Chapter III: The Western Lowland Gorilla; Habitat, Diet and Behavioral Characteristics

THE WESTERN LOWLAND GORILLA: HABITAT AND DIET

Gorilla gorilla inhabits pockets of what were Pleistocene forest refuge regions across the African tropical zone (Tutin and White 1999, refer to Appendix A; Stanley 1996). *Gorilla gorilla gorilla*'s home ranges are located in the western section of these ancient refuge habitats, i.e., from Nigeria to Gabon and within the Congo Basin extension. The WLGs and the high altitude MG are separated by over a thousand miles (Fossey 1983; Emlen, Jr. and Schaller 1963).

Jones and Sabater Pi (1971; see Appendix A, this thesis) in their early ground breaking ecological survey of Rio Muni (Republic of Equatorial Africa) assign the WLG to montane forest or regenerating forest. Tutin (1996) and Tutin and Fernandez (1984) extend the WLG habitat to include primary forests (also see Fay 1997). Deblauwe *et al.* (2003) adds old logging roads and camp clearings to the WLG habitat list. Also noted is that old and young secondary forests differ in tree biomass and undergrowth (Deblauwe *et al.* 2003). THV distribution throughout the WLG tropical forests is widespread, but generally lacks the blanketing and density pattern of the high altitude MG, i.e., THV is sparsely, but widely distributed (Doran and McNeilage 1998; Fay 1997, see Appendix A; Morgan *et al.* 2003; Tutin and Fernandez 1993; Tutin 1996).

All gorilla habitats within the western geographic parameters contain fruit and herbs, important components of the WLG diet (Doran *et al.* 2002, refer to Appendix A; Tutin *et al.*, 1997; Tutin and White 1999; Yamagiwa *et al.* 2003). The herbs may be terrestrial or aquatic (Olejniczak 1994, 1996, 1997; Tutin 1996). Fruit, although seasonally variable in quantity and type, is available in some form and amount throughout the year (Goldsmith 1999a, see Appendix A, 1999b; Remis 1997a; Remis *et al.* 2001). WLG selection and consumption of preferred foods are based on gustatory passage and coding (Hladik *et al.* 2002; Remis 2000), a sensory component (Dominy *et al.* 2001) and nutritional requirements (Goldsmith 1996; Kuroda *et al.* 1996; McNeilage 2001; Magliocca and Gautier-Hion 2002; also see Oates *et al.* 1977). Fallback,

or less preferred but consistently and readily available foods, i.e., leaves, bark and low quality herbs, are eaten as needed (Doran and McNeilage 2001; Remis *et al.* 2001; Tutin 1996) to fulfill absolute body size dietary requirements (Remis 2000; also see Tutin and White 1999).

The two categories of food types, fruit and aquatic herbs, are significant to the WLG, but not the highland gorilla (Doran *et al.* 2002; Doran and McNeilage 1998, 2001; Tutin 1996; Watts 1996). Noted previously is that less than one percent of the MGs' diet is fruit (Kuroda *et al.* 1996 see Appendix A.; Remis 1997a; Watts 1996). Jones and Sabater Pi (1971) refer to the WLGs as being folivorous in the dry season and frugivorous in the rainy season. Kuroda and colleagues (1996) describe the WLGs as opportunistic frugivores, i.e., they eat fruit when they encounter it. However, Doran and McNeilage (1998) argue that WLGs do select the fruit they eat, i.e., they will ignore certain fruits in favor of others and travel to obtain preferred succulent fruits.

Tutin and White (1999) note that WLGs (along with mangabeys and colobus) are transient visitors to fragmented habitats when abundant succulent fruit is in season. Such gorilla visits are less frequent than those of the chimpanzee or mandrills, but this WLG gorilla movement does require crossing savanna that is not part of the natural gorilla habitat (Tutin and White 1999). Furthermore, it is argued that the WLG pursues succulent fruit at the cost of greater day ranges, greater energy use and possible limits on group size (Cipolletta 2003; Doran and McNeilage 1998, 2001; Goldsmith 1999a, 1999b; Remis 1997b; Tutin 1996; Tutin *et al.* 1992; Tutin and White 1999; also see Steudel 2000 for analysis of the individual and group energetic effects of primate group movement and Chapman and Chapman 2000). Therefore, the Kuroda's *et al.* (1996) perspective of the WLG as opportunistic frugivores is likely inadequate in explaining the patterns and consequences of WLGs' fruit consumption. Summarily, the WLG opts for succulent sweet ripe fruit as a preference food (Tutin and Fernandez 1985, 1991; summary, Doran and McNeilage 1998). These choices overlap with sympatric chimpanzees (Kuroda *et al.* 1996; Tutin and Fernandez 1993; Tutin 1996).

The Lope (Gabon) tropical forests are both primary and secondary. Seasonally, the WLG incorporates sixty-two species of fruit into their diet (Tutin 1996). Thirty-five percent of food is harvested arboreally by the WLG. In comparison ninety percent of the MG food is harvested terrestrially (Watts 1984). Tutin (1996) reports having heard WLGs running toward succulent fruit trees while emitting excited vocalizations. Compared to sympatric chimpanzees, the gorillas take little time processing fruit before eating and they swallow large seeds (Tutin and Fernandez 1993; also see Tutin *et al.* 1991, see Appendix A). When fruit is abundant the WLG diet has greater fruit diversification than sympatric chimpanzees (Tutin *et al.* 1992, 1993; also see Kuroda *et al.* 1996). However, the gorilla at Lope tends to avoid fruits of oil palms (high in lipids); these fruits are eaten by the chimpanzee (Tutin and Fernandez 1985; Doran and McNeilage 1998).

Kuroda and colleagues' (1996) research finds that the Ndoki (Congo) gorillas have both the greatest diversity of WLG fruit consumption and the greatest herb availability in comparison to other study areas (e.g., Lope or Mondika; also see Doran *et al.* 2002). The earlier discussed conclusions that the gorilla's digestive system reflects both flexibility in diet and, most importantly, fruit consumption are supported by the Ndoki data. Moreover, the WLGs' preference for fruit as documented at all research sites not investigating specific questions about AHV behavior (for particular sites see Bermejo 1997, 1999; Doran and McNeilage 1998, Fay 1997, Magliocca and Gautier-Hion 2002; McNeilage 2001; Mitani *et al.* 1993; Remis 1997a; Tutin and Fernandez 1993; Tutin 1996) further suggests that fruit in the WLG diet is significant in relation to evolutionary adaptation (see Doran and McNeilage 2001).

Fruit is a "patch resource" (*sensu* Wrangham 1980, see Appendix A) as is AHV. Mbeli Bai (Congo), a swampy clearing of 12.8 hectares characterized by aquatic herbs, is frequented by single silverback-lead groups and lone males for feeding (Fay 1997; Olejniczak 1994, 1996, 1997; Parnell 2002; Stokes *et al.* 2003). Forests of monodominant *Gilbertiodendron dewevrei* (see Blake and Fay 1997, also Appendix A) that change into mixed species primary forest surround the bai. The swampy clearing is saline (*sensu* Magliocca *et al.* 1999) and supplies to the

WLGs, AHV rich in sodium, potassium and other trace minerals (Stokes *et al.* 2003). Magliocca and colleagues (1999, 2002, also Appendix A) note that the dense vegetation surrounding the bai at Maya Nord (Congo) is deficient in trace minerals. They suggest that the saline food permits the completion of nutritional needs for the WLG groups using this resource. No similar published nutritional analysis (known to this researcher) on the Mbeli Bai vegetation is available, but the Maya Nord finding does open like possibilities of saline nutritional benefit to the WLG.

The Mondika site (Central African Republic) has swampy forest and mixed species tropical forest; therefore a full range of food types, i.e., THV, AHV, foliage, pith, bark, invertebrates and fruit are available and used by its WLGs (Doran *et al.* 2002, Doran and McNeillage 2001). One hundred twenty-seven plant food species are used of which seventy are fruits, thirty-three leaves, fourteen stems, two flowers and eight barks in addition to termites, ants and soil-eating are considered (Doran *et al.* 2002). Fruit tree size usage varies. Mondika's fruit score (mean percentage of fruit found in analyzed fecal samples) was thirty-nine compared to forty-eight for Ndoki. Mondika's THV is classified as close-clumped distribution and has decreased density in comparison to MG high altitude habitats (Doran *et al.* 2002; Doran and McNeillage 1998, 2001, Watts 1996). Mondika's gorilla dietary resource distribution base, then, appears to be "clumped" (*sensu* Wrangham 1980) in the major nutritional categories of fruit, AHV and THV.

Bai Hokou (Central African Republic) WLG habitat is dominated by secondary semi-deciduous forest of mixed species; fruit trees and terrestrial herbs are the two most frequent food sources at this WLG location (Goldsmith 1996, 1999a, 1999b; Remis, 1997a, 1997b; Remis *et al.* 2001). During the dry season (January through March) the WLG diet is primarily THV, pith leaves and bark. During the wet season fruit dominates food intake (Goldsmith 1996; 1999a; Remis 1997a). Remis (1997a) notes that fibrous fruits were eaten in the dry season; hence, although varied in type (i.e., fibrous rather than succulent) and quantity, fruit is eaten throughout the year. Remis (1997a; Remis *et al.* 2001) also found that when available, succulent fruit is the

preferred food and eaten in large quantities by WLGs at Bai Hokou. From a detailed analysis of the nutrient content of folivorous and frugivorous dietary items Remis and colleagues (Remis *et al.* 2001) conclude as follows:

1. The frugivore-folivore mixed dietary intake of the WLG “provides the most suitable nutrient balance for gorillas and many other herbivores” (p. 825).
2. The Karisoke (high altitude MG) diets “are distinctive; even lower altitude mountain gorilla diets are all more diverse, and include a variety of fruits and leaves from woody species” (p. 825; also see Goldsmith 1999a).

To be noted is that aquatic herbs are not found at Bai Hokou; consequently, their role in nutritional balance is not included in obtaining dietary balance (see: Magliocca *et al.* 1999; Magliocca and Gautier-Hion 2002; also related annotations in Appendix A)

Lossi’s WLGs (located approximately 50 km² south west of Odzala National Park, north Congo) are most evident in the open-canopy Marantaceae forest although nests are also visible in primary forests. In addition, clearings and savannas are present in the Odzala National Park region (Bermejo 1999a, 1999b; also see Fay 1997). Bermejo’s (1997) dietary observations of Lossi gorillas are consistent with other WLG sites, e.g. Maya Nord or Mondika, i.e., fruit, THV and saline clearings provide sufficient and necessary nutritional intake to the WLG groups.

Finally, the WLGs within southeast (Ebo forest) and southwestern (Cross River which includes an area in Nigeria) sections of Cameroon have little published literature detailing dietary analysis. Deblauwe *et al.* (2003) investigated insectivory (using fecal analysis) of the WLG in the Ebo forest. The habitat included primary, secondary and riverine forests as well as old logging roads and swamps. In addition to insect intake analysis Deblauwe and colleagues (2003) noted green leaf fragments, fiber, small seeds and large fruit seeds in the fecal samples. No nutritional analysis on swamp vegetation was done. Mitani and coworkers’ (1999) investigation on dispersal of fruit seeds in southwestern Cameroon on 276 square hectares of evergreen forest found the chimpanzee present. However, the WLG was no longer evident in the area. This supports a

general view of a nearly extinct gorilla population (Cross River, approximately 250 individuals) on the Cameroon-Nigerian border (see Morgan *et al.* 2003 for summary). In Morgan and colleagues' discussion (2003) of Cross River gorillas, fecal analysis, consumption of fiber, green leaf fragments, fruit and fruit seed and remains of stem pith were also recorded. No other dietary information was given.

Sympatric chimpanzee with dietary and range overlap reside with the WLGs, e.g. at Lope, Ndoki and Lossi (see Kuroda *et al.* 1996; Tutin and Fernandez 1985, 1991; Doran and McNeilage 1998). As stated earlier the diversity of fruit used by chimpanzees is less than that used by WLGs. However, Kuroda *et al.* (1996; see Appendix A) finds that gorillas are less persistent in their fruit eating than chimpanzees, i.e., WLGs seldom fulfill the optimal foraging hypothesis in relation to clumped (tree) fruit (Goldsmith 1999a; also see Yamagiwa *et al.* 1996). Other diet differences between the chimpanzee and WLGs are evident, e.g., gorillas, but not chimpanzees, consume bark seasonally (Kuroda *et al.* 1996) and WLGs eat a diverse range of vegetation species and types (e.g., mature leaves) that chimpanzees do not. Moreover, chimpanzees do not participate in seeking out and consuming aquatic herbs (Doran and McNeilage 1998). Doran and McNeilage (1998) raise several issues or questions based on the dietary practices of the WLG and sympatric chimpanzee with reference to the MG.

First Doran and McNeilage (1998) suggest that the greater clumping in the distribution of WLG food should produce more scramble competition than within the MG groups. Furthermore, WLG groups should be smaller or they should forage over a larger area than the MG. Because of ecological and dietary differences, Doran and McNeilage (1998) raise the possibility of differences in the social system between the WLG and MG. However, the Doran and McNeilage question is framed in relation to the chimpanzee, i.e., they question if the WLGs' use of fruit demonstrates that the WLG social system is closer to that of the chimpanzee (fission-fusion) than to that of the MG (cohesion). In the next section of this chapter the issues raised and the questions

asked by Doran and McNeilage (1998) are examined by investigation of WLGs' groupings, foraging strategies and behavioral characteristics.

WESTERN LOWLAND GORILLA: BEHAVIORAL PARTICULARS AND SOCIAL SYSTEM

Group size and composition as well as spatial relationships constitute the social organization of the WLG group (*sensu* Keppeler and van Schaik 2002). The mean group size varies from Mbeli Bai at 6.6 (Parnell 2002) or 7.5 (Olejniczak 1996) to 14 at Lossi (Bermejo 1997, 1999b; also see Doran and McNeilage [1998] for mean group size reviews for Lope, Bai Hokou, Ndoki, Lossi, Mbeli, and Karisoke; the Mbeli Bai and Lossi means vary from above). The Doran and McNeilage (1998) stated mean group size for Karisoke is 9.15. The WLG and MG (Karisoke) average group sizes are not significantly different (Doran and McNeilage 1998; Tutin *et al.* 1992; Yamagiwa *et al.* 2003).

Moreover, Bermejo (1997, 1999b) states that group size is not constrained by within group competition for fruit. However, Parnell (2002) maintains that the WLG group size is smaller when fruit is the primary food resource (i.e., during times of abundant fruit), but not when THV is the major food resource. Doran and McNeilage (1998) argue that due the WLGs' dietary addition of fruit and its clumped distribution, the upper limits of group size may be restricted. In short, it is unclear if fruit consumption is correlated to any upper limit on group size. As described in chapter two of this thesis, problems of visibility, habituation and tracking have made it difficult to gather a necessary data base.

Group composition of the WLGs and the high altitude MGs differ in specific ways. First, Doran and McNeilage (2001) find that multi-male groups (i.e., groups with more than one silverback) are not evident in WLG groups as they are in MG groups (Watts 2000a; also Magliocca *et al.* 2002; Parnell 2002, Stokes *et al.* 2003). At Mbeli Bai, according to Parnell (2002), no multi-silverback groups are evident. Parnell argues that past observations of multi-male groups was likely result a male maturing within his natal group and although leaving (as he

became a silverback) sightings occurred shortly before emigration. Second, all-male (bachelor) groups found within the MGs' social organization are not found in the WLGs social system (Stokes *et al.* 2003; Tutin 1996). However, solitary silverback WLG males are frequently seen (Olejniczak 1994, 1997; Remis 1997b; Stokes *et al.* 2003). Doran and McNeilage (1998) recorded that from 1995 to 1996, sixty out of one hundred and sixty-five gorilla contacts at Bai Hokou were lone male gorillas. Generally, males appear to be solitary before acquiring females (Doran and McNeilage 1998; Doran *et al.* 2002; Parnell 2002; Stokes *et al.* 2003; Yamagiwa *et al.* 2003).

Access to fruit trees is a variable in determining WLG grouping patterns (Kuroda *et al.* 1996; Goldsmith 1996). The WLGs use small, medium, large and very large fruiting trees. Tree size determines how many of the foraging group can actually forage arboreally for fruit. Those that do not obtain a place in the tree forage terrestrially (for THV). Therefore, tree size sets limits on arboreal and terrestrial foraging sub-group sizes and the grouping patterns, i.e., as to age and sex in the sub-group (for summary, Doran and McNeilage 1998; also see Kuroda *et al.* 1996). Due to the large body size of gorillas, medium to very large trees are preferences accommodated to foraging strategies (Doran and McNeil 1998). Kuroda and colleagues' (1996) find the gorillas that obtain feeding spots in the fruit trees eat for only a short time period and depart while significant quantities of fruit remain. The explanation may lie in sparse THV, i.e., fruit eating gorillas move on with the THV eating gorilla when the THV patch is depleted (Kuroda *et al.* 1996; contra, Goldsmith 1999a, 1999b).

Tutin *et al.* (1997) argues that within tropical forests, the species and flora communities are usually synchronic; therefore, substantial seasonal variations occur as to size of the fruit tree and quantity of fruit. During fruit scarcity, keystone food, largely THV (but also leaves, figs and bark) are consumed (Cipolletta 2003; Fay 1997; Goldsmith 1996b; Tutin 1996; Tutin *et al.* 1997). The forage ranging issue is complex; the parsimonious answer may not be sufficient (Goldsmith

1999b). However the accumulated data on the WLG suggest that groups travel further when fruit is abundant (Doran and McNeilage 2001; Tutin 1996; Remis 1997b).

Goldsmith's (1999a) analysis of WLG daily path travel at Bai Hokou confirms that fruit influences path length (also, Bermejo 1997, 1999b [Odzala]; Cipolletta 2003 [Ndoki]; Tutin 1996 [Lope]). Initially termite availability as well as seasonally preferred fruits appeared to sway the use of longer daily foraging paths, but data showed that termite nests were visited more frequently when frugivory was the dietary pattern than when folivory was dominant (dry season) (Goldsmith 1999a). Goldsmith (1999a) concluded that longer daily group travel was related to the food preference for fruit and the termite dietary use was incidental.

In addition to fruit, AHV consumption, predation and sleeping site choice influence foraging strategies (Fay *et al.* 1995; Goldsmith 1996; Olejniczak 1994, 1996, 1997). Swamp AHV is nutritionally (ecologically) and socially significant when available to WLG groups and lone males (Olejniczak 1996, 1997; Parnell 2002; Stokes *et al.* 2003). Magliocca and coworkers (1999, 2002) found that WLGs traveled ten miles through high density THV Marantaceae forest to reach Maya Nord to feed on saline herbs. Moreover, Janson and Goldsmith (1995) argue that travel time and length of daily paths are also influenced by predatory pressure. According to Fay *et al.* (1995) there exists pressure of leopard attacks. Goldsmith (1999a) observed leopard prints on three occasions near gorilla groups. Additionally, according to Goldsmith (1996), preferred sleeping sites (although few in number, i.e., usually located where light gaps occur in the canopy) are factors in foraging strategies (with admittedly no quantitative data).

Cipolletta (2003) summarizes the non-parsimonious perspective on WLG ranging behaviors as follows:

Ranging behavior is likely to be affected by different pressures and no factor alone can account for the patterns a group displays, though, at any given moment any one factor may alone play a stronger role. During the study, habitation seemed to be the single most influential factor affecting the group's day ranges, thereby concealing the relationship between ranging and fruit consumption. (p. 1222)

Generally, however, data support the conclusion that WLGs have longer daily travel than do MGs and that fruit consumption (with preference for succulent fruit) is at least seasonally a factor in the longer travel pathway (Goldsmith 1999a; Remis *et al.* 2001; Watts 1991). Additionally, Yamagiwa *et al.* (2003) proposes that generally WLG groups have a larger home range than MG groups.

Doran and McNeilage's (1998) earlier stated prediction that clumping of resources should produce either smaller groups of WLG in comparison to MG groups or should lead to larger foraging areas, appears to tentatively hold in relation to the larger foraging areas. As seen in the previous discussion on WLG group size, the former prediction lacks credibility. Caution is needed, however. Although the latter prediction has support, it is founded mainly on indirect evidence (with problems of habituation and visibility as described in chapter two). On-going studies at Lossi where some habituation has been completed and where the visibility is also somewhat better than at other WLG sites (Bermejo 1999a, 1999b) may further support (or not) the Doran and McNeilage prediction on larger foraging areas for the WLG.

In addition to clumped fruit, there is also clumped AHV and records of THV as clumped or sparse in WLG habitats. At Mondika and Lope the THV is clumped, but closely distributed (Doran *et al.* 2002; Tutin 1996; Tutin *et al.* 1997) while at Ndoki THV is sparse and widely spread (Kuroda *et al.* 1996). It is not surprising, therefore, that WLG groups' cohesion differs in significant ways from that of the MG (Bermejo 1997, 1999b; Doran and McNeilage 1998; Magliocca *et al.* 1999; Remis 1997a, Remis 1997b; Tutin 1996). At Lope the WLG groups are said to be 'cohesive', but are observed to have a large spread between members (although not beyond vocal range) (Tutin *et al.* 1991; Tutin and Fernandez 1993; Tutin 1996). Tutin (1996) infers a flexibility in spatial/temporal social units that differs from that of the MG. From the perspective of the numerically larger subspecies, *Gorilla gorilla gorilla*, this aspect of social organization (*sensu* Keppeler and van Schaik 2002; also see Keppeler 2001) is at variance by *Gorilla gorilla beringei* whose spatial/temporal foraging strategies differ.

At Mondika a lone female gorilla was sighted as well as females foraging more than one hundred meters from males (Doran and McNeilage 1998). Mitani and coworkers (1993) have noted lone females on occasion in the Ndoki forest. In addition sub adults have been observed several hundred meters apart from the primary foraging group near Lossi (as reported in Magliocca *et al.* 1999 from personal correspondence with Bermejo). Also at Lossi large groups (to thirty-four individuals) with one silverback can be spread sufficiently apart that clapping is used to communicate (Bermejo 1997, 1999b; see Stokes *et al.* 2003; Doran *et al.* 2001). Various researchers report gorilla sub groupings during foraging, for example, Goldsmith (1996) and Remis (1997b) at Bai Hokou or Doran and McNeilage (2001) at Mondika. Frugivory and sparse distribution of fruits may influence WLG to disperse during foraging (Goldsmith 1996; Remis 1997b; also see Tutin 1996). Earlier discussed ELG female groups without silverback leadership (Stanford and Nkurunungi 2003) lends increased possibility that the more cohesive and consistently lead silverback groups in the Virunga highlands represents a type of social organization at the far end of a spectrum within the *Gorilla gorilla* species.

Within the saline, swampy clearings supergroups are possible (Olejniczak 1996, Parnell 2002; Parnell and Buchanan-Smith 2001; Stokes *et al.* 2003). Data indicate that more than one group (and lone males) simultaneously forage within the large clumped AHV at Mbeli Bai, i.e., supergroups may form (Olejniczak 1994, 1996, 1997; Parnell 2002; Stokes *et al.* 2003) and Maya Maya (Magliocca *et al.* 1999). Contrarily, Bermejo's (1997) documentation during maximum fruiting periods cites incidents of groups nesting together for one or several nights, but separating to forage. The inference is that whereas there may be contests for fruit access (especially between gorilla groups), there is no contest for access to AHV (Olejniczak 1996).

Supergroup formations, daily WLG use and the openness of Mbeli Bai support information gathering on between group encounters and female dispersal (Olejniczak 1996; Parnell 2001, 2002; Stokes *et al.* 2003). Olejniczak (1996) observed a variety of silverback male reactions during inter-group encounters. Proximity of feeding followed by avoidance, peaceful

intermingling or assertive water displays by silverbacks are all possible options as well as silverbacks and group members transferring from one type of behavior to another (Olejniczak 1996; Parnell and Buchanan-Smith 2001; Stokes *et al.* 2003). Magliocca *et al.* (1999) emphasizes peaceful intermingling at Maya Maya although agonistic behavior may occur. Tutin's (1996) data confirm similar reactions with WLG groups meeting in overlapping THV foraging areas at Lope. Contrarily, Sicotte (1993) finds that with MG less than seven percent of fifty-eight observed intraspecific encounters were peaceful. Doran and McNeilage (2001) conclude that WLG intragroup encounters may be more frequent and variable than MG encounters and perhaps closer in similarity to *Pan paniscus* than to *Pan troglodytes* (see Strier 2003 for overview of *Pan* species differences in intraspecific group meetings).

Between February of 1995 and July of 2001, Stokes and co-researchers (2003) monitored twenty WLG groups and recorded data on female transfers (only such published study on WLGs to date). Because tracking of groups was not possible (see chapter two, this thesis) a midpoint transfer date was assigned. The midpoint was established between the date the particular group was last seen prior to change in female composition and the first observation of the group with the change. Stokes and colleagues (2003) inferred from the collected data the following:

1. Female natal and secondary transfers are common among WLGs (which is consistent with female MGs).
2. Larger gorilla groups are losing females and smaller groups are gaining females although when transferring between groups there was a "show of preference for significantly smaller groups" (p. 329). Furthermore, reproductive disadvantage for the mature female gorilla was possible when they resided in very large and very small groups.
3. Also consistent with female MG transfer analysis (see chapter one, this thesis) male quality and ability to protect the female was important to transfer decisions.

Moreover, Stokes and coworkers (2003) noted that in accordance van Schaik's (1989) theory, i.e., within-group food competition (contest) predicts female philopatry; the voluntary dispersal of the female lowland gorilla suggests intragroup resource competition is low.

According to Stokes and coworkers (2003) although female counter-strategy to infanticide (seeking protection from a quality silverback group leader) has no direct evidence, there is indirect evidence. First, they found no incidents of females transferring with unweaned infants to other groups except upon death of a group's alpha silverback (with the result of the infant 'disappearing'). Second, Stokes *et al.* (2003) referred to observations that infanticide in MGs concluded with the female breeding to her new silverback leader, thus completing the male infanticide strategy (Watts 1989, Sterck *et al.* 1997; see Dunbar 1988 model as alternative to van Schaik's 1989 model as basis of Sterck *et al.* 1997). WLG behavioral studies are in their infancy (Doran and McNeilage 1998, 2001). However, Stokes *et al.* (2003) research, analysis and review of female voluntary dispersal in WLG are indicators that the behavior is evident in all three gorilla subspecies and, therefore, may be considered a defining characteristic of the species *Gorilla gorilla*.

Moreover, Stokes *et al.* (2003) confirm WLG male dispersal from the natal group. Again, as with female dispersal, what is reported to be a primary characteristic of *Gorilla gorilla* is documented within all three subspecies (Robbins 1995; Stanford and Nkurunungi 2003; Stokes *et al.* 2003; Tutin 1996; Watts 2000a). Although aspects of both social organization and social structure (*sensu* Keppeler and van Schaik 2002) may vary between gorilla subspecies, it also seems that fundamental defining characteristics (i.e., male and female dispersal from natal groups) of the gorilla social system are consistent across the MG, ELG and WLG populations. However, Stokes and colleagues (2003) also argue that as with mature male MGs, mature male WLGs use infanticide as a fitness strategy. There is no evidence direct or indirect to support infanticide as a mature male fitness strategy within the ELG social system. Stokes and coworkers (2003) rely on the socio-ecological model to interpret indirect data and reach the conclusion of

risk of infanticide for the WLG female significantly influences her sociality. In chapter four the infanticide issue is again elaborated.

Chapter IV: Discussion

In all western African gorilla habitats, “less cohesive” is used to describe the WLG’s foraging groups when compared to MG foraging groups (Kuroda *et al.* 1996; Doran and McNeilage 1998). For example, at Lope, Tutin (1996) finds the WLG foraging spread to be as much as five hundred meters. Goldsmith (1996) and Remis (1997) suggest a correlative relationship between frugivory (accompanied with sparsely distributed THV) and less group cohesion, i.e., an ecological premise is used to explain the social organizational difference between the WLG and MG. Such a correlation, although supportive of Wrangham’s (1979, 1980) ecological orientation, is insufficient to explain the variations within the three subspecies’ social systems (*sensu* Keppeler and van Schaik 2002) when the variations include a lack of recorded or observed acts of infanticide (ELG), significantly more peaceful intermingling among separate groups of WLGs and social structure differences between the WLG and MG groups.

In addition to a general lack of tight cohesion in WLG foraging groups, both subgroupings and supergroupings are evident in WLG communities, but not in MG groups (Doran and McNeilage 1998; Sicotte 1993). Supergroupings appear more prevalent in and around swampy or saline forest clearings (Magliocca and Gautier-Hion 2002; Olejniczak 1994, 1996, 1997; Stokes *et al.* 2003). Subgroupings of WLG are most likely in sparse, clumped THV or as the group partitions with some members foraging arboreally while others forage terrestrially, for example, as described by Kuroda *et al.* (1996) at Ndoki. Sequential supergrouping followed by subgrouping may occur during intraspecific nesting in overlapping ranges during fruiting season. Supergroups may form at night and separate at daylight, followed by the base groups subgrouping to take advantage of ripe fruit trees while others forage for THV (Bermejo 1997, 1999b; also Tutin 1996). Subgrouping is rare among MGs (Watts 2000b). Structural grouping variations (to be discussed) raise additional questions within the socio-ecological model.

Fay (1997) and Kuroda *et al.* (1996) argue that WLG grouping and distribution is predicated by ground vegetation. I suggest such a conclusion may be simplistic. Goldsmith (1996,

1999a, 1999b) emphasizes the influence of fruit and its seasonality on daily path lengths; Yamagiwa *et al.* (2003) finds that WLG annual home ranges reflect succulent fruit preferences and usage. Cipolletta (2003) suggests not only fruit, but also the presence of researchers themselves as variables creating WLG movement patterns. Additionally, preferred nesting sites and predator avoidance (Fay *et al.* 1995; Goldsmith 1996, 1999a) are cited factors for direction and length of group travel.

As discussed in Tutin and White (1999), extant gorilla habitat and distribution reflect the adaptations to changing forest conditions and resource availability of approximately 18,000 years ago. Although ground vegetation was a significant factor, shrinking forests also created new factors in prey-predator density ratios (also see Stanley 1996) and, for the WLG, suitable nesting sites (remembering that WLG often nest arboreally). Parsimony may not be sufficient to explain the gorilla patterns of distribution and grouping. Moreover, Doran and McNeilage (1998) suggest that grouping, movement pattern and distribution differences among the subspecies (e.g., female groups without a leader [ELG], less cohesion in foraging [WLG] or multi-bachelor groups [MG]) reflect shifting balances that depend upon ecological, demographic and interactive social influences.

At this point, the simple answer to the Doran and McNeilage (1998) query of whether or not the WLG social system was closer to that of the chimpanzee rather than the MG is no. Despite reduced group cohesion and the occurrence of sub and super groupings, I suggest that social flexibility rather than fission-fusion best accounts the variations among the gorilla subspecies. Fay (1997) refers to **similar** social systems among the three gorilla subspecies. Intersubspecies diversity (*sensu* Keppeler and van Schaik 2002) exists within aspects of social organization (e.g., greater spatial-temporal distances for the WLG) and social structure (e.g., WLG absence of bachelor groups), but not in the mating system. What Watts (1992, 1996, 2000a) finds as the determining core of the extant gorilla social system, the male-female mating bond within a multifemale-one alpha silverback group remains consistent across all three subspecies.

The characteristics identified by Wrangham's ecological model (1980), i.e., non-bonded, non-hierarchical female-female relationships, female dispersal and (in addition to the Wrangham model) male dispersal are also primary to all three subspecies' social systems. Succinctly, I argue that (within the present data) dietary and resource diversity generate variation in gorilla sociality, but do not create different social systems. If variations in habitat, diet and social structure/organization are viewed within a range of possibilities for the species and not within the particulars of high altitude MG, the *Gorilla gorilla* social system then may be seen as a reflection of the geographic division among the species and the ecological and social consequences. Doran and McNeilage (1998) extend a continuum perspective to include the chimpanzee as follows:

If we consider a continuum of ape dietary and social patterns, chimpanzees (as fruit pursuers with flexible grouping patterns) would be at one extreme and mountain gorillas (as herbivores with large, cohesive groups) would be at the other end. The place of the western lowland gorillas on the continuum may shift both seasonally and across sites... Lowland gorillas would be most similar to mountain gorillas on the continuum, albeit with greater group spread. (p. 129)

Perhaps the last line above might better read: "Mountain gorillas would be most similar to lowland gorilla on the continuum, albeit with less group spread."

Across and within the gorilla subspecies are the use of non-preferred THV, mature leaves and bark for fallback foods as well as THV as a portion of the daily diet. The consistent reliance by *Gorilla gorilla* on non-fruit foods underlies a variation in frugivory between sympatric chimpanzees and gorillas. An increased or substitutional use of non-fruit staple food choices during low fruiting times explains why stability in gorilla social organization (*sensu* Keppeler and van Schaik 2002) and some degree of group cohesiveness are consistent in gorilla groups compared to the fission-fusion of chimpanzee groups.

Gorillas do not become solitary-like foragers as do chimpanzees (see Tutin 1996), i.e., chimpanzees use fission as a mechanism to seek out and consume preferred fruit during times of scarcity. As previously discussed (p. 28, this thesis) although both chimpanzees and sympatric gorillas increase non-fruit consumption in times of fruit scarcity, only the chimpanzees persist in

locating rare clumps of fruit in an attempt to retain fruit as a primary food source (Kuroda *et al.* 1996).

However, Wrangham (1979) argued that for the female MG with the use of THV as fallback food and as a staple food, gregariousness is less costly than for other more frugivorous female apes (e.g., chimpanzees). THV's lack of seasonality and dense blanketed availability require minimal energy to locate and harvest while travel costs for frugivores are greater. The general density also allows for sufficient calories for each member of the group. Watts (1996) also questions the social effects of WLG frugivory on female gregariousness. Doran and McNeilage (2001) suggest a need to gather information on female-female relationships at frequent intergroup encounters during AHV consumption and during meetings in overlapping ranges that contain preferred fruits. They also recommend investigation of possible infanticide increase as a result of intergroup mingling and research on whether or not more female kin reliance occurs within WLG groups than within MG groups. Doran and McNeilage (2001) and Watts (1996) emphasize that data are currently not available in relation to the WLG on these topics.

Earlier I stated that additional questions needed to be raised in relation to the socio-ecological model. As above it has been seen that Watts, Doran and McNeilage note not only a lack of data on certain topics, but also that within those topics serious questions are raised about gorilla female gregariousness and the consequences. Most significant is that *prima facie* the issue of infanticide is a significant problem. The questions are:

1. Does infanticide extend across all three subspecies?
2. What are the consequences to the socio-ecological model if infanticide variation exists?
3. Are there consequences to the stated importance (Watts 1996) of infanticide in *Gorilla gorilla's* social evolution if infanticide is not consistent across the gorilla subspecies?

The observations of the ELG's leaderless female groups, sightings of lone WLG females, the lack of WLG group cohesion (in comparison to the MG) and thereby less female protection, the extensive intraspecific mingling of WLG groups at AHV sites and in overlapping areas during fruiting season, raises a myriad of contradictions within the socio-ecological model (review in Doran and McNeilage 2001). Male infanticide as a fitness strategy is not universal among primates. Neither male bonobos nor orangutans, for example, are known to use infanticide (Watts 1996). Watts (1996) speculates that bonobos have little sexual dimorphism, which may be a factor. However, there is significant sexual dimorphism between male and female orangutans while chimpanzees (who do commit infanticide) have somewhat less sexual dimorphism.

However, although questions may be asked about infanticide (as above), insufficient data exist to provide sufficient and verifiable answers. As previously noted, beyond the initial behavioral research at Mbeli Bai (Stokes, Olejniczak and coworkers 2003) and at Lossi (by Bermejo 1999b), little other behavioral data on WLG are gathered. Furthermore, tracking, habituation and solutions to a lack of visibility at most WLG sites seem essential tools in answering social questions and in accomplishing significant long term research on both ecological and behavioral patterns of the WLGs and ELGs.

Moreover, the clumping of resources within the WLG habitats and the consequence to the ecological perspective (*sensu* Wrangham 1980) now requires further comment. At the start of this thesis it was argued that Wrangham's ecological perspective is embedded in socio-ecological models, e.g., Sterck *et al.* 1997. Within Wrangham's (1980) theory is the premise of particular consequences of resource distribution to female-female relationships, i.e., resource clumping and blanketing produce different social results. This conclusion is not consistent with the research on the WLG in comparison to MG. As previously discussed, although the WLG female, at least seasonally, consumes primary clumped resources (fruit and AHV) in contrast to a female MG with blanketed, dense THV, each remains consistent in characteristic behavior patterns, e.g., natal dispersal and non-bondedness to other females. Again, a change of perspective may alter the

difficulties, i.e., using the dietary flexibility of the WLG set as norm. The combination of THV, fruit, AHV (absent in Lope and Bai Hokou), leaves, stems, bark, pith, seeds, soil and insects (despite different emphases in different seasons) provides 'a blanketed' food resource as do the THV, bamboo, leaves, stems, bark, pith seeds, soil and insects for the high altitude MG.

However, from Wrangham's (1979, 1980) perspective a combined foods base is not a factor.

Asking questions about 'diet' separate from 'type of food' are little evidenced in the examined literature. As cited earlier in this paper, Doran and McNeilage (1998) propose a continuum that includes the gorilla and chimpanzee dietary patterns. The continuum moves from fruit-pursuers with flexible grouping patterns to MGs with cohesive grouping patterns. Within this continuum the WLGs would move closer to the chimpanzee during the height of fruiting season and toward the mountain gorilla during the dry season when succulent fruit is scarce. I suggest that such a continuum does not address the variety within the WLG diet, the use and consequences of the swamps (bais) for aquatic herbs nor Wrangham's fundamental premise of teasing out clumped resources as a mechanism for gregariousness. The latter is a primary category to be contrasted with non-clumped blanketed vegetation as necessary in understanding the evolution of the gorilla social system. More intensive study of low altitude gorilla habitats, longer behavioral studies incorporating direct observation of WLGs, asking questions that hypothesize within a continuum perspective and a continuation of testable hypotheses appear essential for understanding *Gorilla gorilla's* social system across subspecies, across habitats, across time and in comparison with other sympatric primate species.

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Appendix A: A Selected Annotated Bibliography on Flora and Some Fauna Species Present
within Particular *Gorilla gorilla* Sites in relation to *Gorilla gorilla* Diet and Ecology

INTRODUCTION

Doran and McNeilage (2001) find that inter-site differences for the WLG in contestable preferred food (e.g. succulent fruit), difference in herb density and the availability and use of bais clearings for AHV require ongoing work to make it possible “to gain a clearer understanding of ecological influences on gorilla behavior” (p. 141). However, as stated in chapter two (p.16, this thesis) data gathering on the ecological issues involving habitat and diet, has been the primary focus of research on the WLG. The twenty annotated articles (below) are representative of the habitat/dietary information and its significance to WLG research. The MG and ELG are minimally included as an indication of cross-subspecies, cross-site and cross-habitat contrasts. However, this annotated bibliography also serves a structural research purpose, i.e., to obtain a balanced presentation within the two major research categories, ecological and behavioral, which, in fact, are not balanced across the gorilla subspecies.

Historically, the Karisoke research on the MG has set the perspective of *Gorilla gorilla*. When necessary the theory generated from this research is used to explain unexamined aspects of the WLG social system (e.g. see Stokes *et al.* 2003 on infanticide and ecology). A literature review of preset limited length on *Gorilla gorilla* and with emphasis on the most numerical subspecies, *Gorilla gorilla gorilla*, may detail and emphasize criticisms in applying MG research to the WLG or may be oriented toward a fairly large body of ecologically based studies. Neither approach, I argue, allows for the fullness of the available gorilla research.

Another alternative is to attempt to balance these two factors (in relation to both the MG and the WLG), while conveying to the reader the efforts and research directions of the WLG ecological (dietary and habitat) analysis to date. Included in the latter is the immense importance of ecological research to the current understanding of not only the WLG, but also to

understanding the concerns, needs, questions and direction of future research on *Gorilla gorilla*. By inclusion of a limited annotated bibliography related to the body of a thesis (which is primarily issue-structured), I suggest that the history, research literature and its consequences in the understanding of *Gorilla gorilla* are given a more robust foundation.

MOUNTAIN GORILLA

Karisoke Research Center, Virunga Volcanic Region, Rwanda
Fossey, Dian 1983. *Gorillas in the Mist*. Boston: Houghton Mifflin.

Appendix A (p. 245) of Fossey's book contains lists of vegetation consumed by four MG study groups at Karisoke sites. Of particular interest is the categorization by type, i.e., fern, grass, herbaceous, shrub, tree, parasitic (fungus and lichens) and vine in relation to species' name; for those unfamiliar with the botanical names of African flora, the food type marker acts as a guide. This is the only mention of fungus or lichens as food source for gorillas although lichens likely have a positive nutritional role [Sara Edwards 2004, personal contact]). Furthermore, on page 50 a map shows the locations of the vegetation zones around Mount Visoke, one of the Virunga peaks, and the ensuing alpine, bamboo, herbaceous, meadow, nettle and saddle zones. Page 51 contains very basic information on dung, dirt, bark, roots and grubs as food. Although Fossey's information is both somewhat incomplete and limited in geographic scope, the food type list is quite helpful when starting an ecological study of mountain gorillas. Furthermore, in addition to the unique mention of lichens as food, the listing of dung and regurgitated/reingested foods as sources of secondary nutrition is mentioned (also rarely discussed by other researchers). It appears that Fossey's long-term close contact and direct observations of the studied groups opened a breadth on gorilla nutrition rarely found in other gorilla dietary literature.

Watts, David P. 2000b. Mountain gorilla habitat: Use, strategies and group movement. In *On the Move: How Animals Live in Groups*. (eds.) Boinski, S. and Garber, P. A., Chicago and London: The University of Chicago Press. pp. 351-374.

Watts gives a detailed overview of the MG flora in relation to forest type, density, preference, altitude of growth, biomass and protein value. Watts notes that MGs deplete resources while they forage, but can also stimulate food production by fertilized seed distribution. Of significance is the relationship between the intensity of particular vegetation zones use and the zone's food abundance and quality. Such material is important in understanding MG social organization and structure in reference to the socio-ecological model, e.g., Sterck *et. al.* 1997. Watts found little to no fruit in the MG diet and seasonality as a dietary issue limited to bamboo shoots, a preferred food if the group has a bamboo forest within their home range. Table 13.2 summarizes examples of significant relationships between aspects of habitat use and characteristics of the food supply. The summary provides a foundation for comparison with the MGs' diets in Bwindi Impenetrable Forest(see below) and/or dietary information on the WLG or ELG. Finally, Watts' examination of altitude in relation to vegetation type is significant to understanding the dietary variation among the *Gorilla* subspecies.

Bwindi Impenetrable Forest, Uganda

Stanford, Craig B. and Nkurunungi, J. Bosco. 2003. Behavioral ecology of sympatric chimpanzees and gorillas in Bwindi Impenetrable National Park, Uganda: Diet. *International Journal of Primatology*. 24(4): 901-918.

Stanford and Nkurunungi's plant species' table (pp. 909-910) pertains to the species of flora eaten by both Bwindi gorillas and chimpanzees. Who eats what flora species and which parts (e.g., stem, leaf or flower) are specified. For the researcher not knowledgeable in flora species' names in relation to flora type (i.e., tree, plant, vine or bush), the use of columns defining the section of each flora consumed (e.g., pulp, seed, leaf, etc.) is often sufficient to identify type. Furthermore, fungus, bark or wood is designated when appropriate. Of interest is the data on flora dietary differences or overlap between sympatric chimpanzees and gorillas in Bwindi and the higher altitude MGs. This work establishes fruit as a major item in the MG diet at lower altitudes thereby implicitly challenging the perspective of *Gorilla gorilla beringei* as a subspecies having an almost exclusive a THV diet. The need to consider locale and altitude in relationship to diet is

evident. In addition, since fruit is a clumped food resource, questions are therefore raised about how the researcher relates food distribution to primate social systems.

WESTERN LOWLAND GORILLA

Rio Muni, Republic of Equatorial Guinea

Jones, Clyde and Sabater Pi, Jorge. 1971. *Comparative Ecology of Gorilla gorilla (Savage and Wyman) and Pan troglodytes (Blumenbach) in Rio Muni, West Africa*. New York: S. Karger.

Jones and Sabater Pi provide a table (p. 13) of plant species and percent of individual frequency as applied to a specific location near Mt. Okoro Biko, Rio Muni (list compiled from the Forest Service of Rio Muni botanical data surveys). The table does not contain all species in the designated area, but only those of which the forest service had records. In addition, the record does not stipulate which flora species are foods for the WLG nor does it include any suggestions as to the type of flora (i.e., plant, bush, tree, vine, etc.). However, page 72 does contain a table of the major food plant species and the parts eaten. Unfortunately, this compilation is limited in breadth. Within the text there is some rationalization of foliage for nest and bedding use and analysis of the fruit genus, *Aframomum* (also see Doran *et al.* 2002, as below). The latter is significant because it represents a major preferred food source that distinguishes the type of dietary intake between WLG and the high altitude MG, i.e., the frugivorous intake of the WLG not present in the MG. This study is of historical importance for it is one of the earliest to suggest an ecological difference between the eastern and western gorilla subspecies within a published work of specific data in relation to an ecological survey in western Africa. However, it should also be noted that as these lists date to 1971 (or earlier), human-made and natural processes may have created significant alterations in the particular habitat.

Maya Ford, Parc National d' Odzala, Republic of Congo

Magliocca, Florence, Querouil, Sophie, Gautier-Hion, Annie. 1999. Population structure and group composition of western lowland gorillas in north-western Republic of Congo. *American Journal of Primatology*. 48: 1-14.

Magliocca and colleagues' research paper's purpose is to examine size and group composition of the WLG in Maya Nord, a clearing with swampy attributes. However, this article

also contains information on the herbaceous composition and saline content on this area, which was traditionally exploited for salt by local fauna. Historically, the clearing was shared by WLG, the forest elephants, forest buffaloes and giant forest hogs. Gorillas visit daily to feed on sodium rich plants (approximately 60% of their feeding time at Maya Nord) within a time range of two minutes to four hours twenty-three minutes (mean, one hour eighteen minutes). Magliocca, *et al.* provide the majority of scarce data on the use of saline herbs in the Maya Nord. This researcher found the Magliocca *et al.* article of prime importance in concert with the Magliocca and Gauthier-Hion 2002 publication (below). The appeal of swamp-like openings to the gorillas was not only a lack of elephant poachers (also a threat to the gorillas), but also the provision of necessary minerals that were deficient in the surrounding THV vegetation. *De facto* the mineral analysis questions the assumption that densely distributed THV necessarily provides gorilla populations with sufficient nutritional intake (see below).

Magliocca, Florence and Gautier-Hion, Annie. 2002. Mineral content as a basis for food selection by western lowland gorillas in a forest clearing. *American Journal of Primatology*. 57: 67-77.

Magliocca and Gautier-Hion include three useful tables in their presentation. The first is a plant inventory (p. 72) that contains family and species names and a scaled abundance rating of each species in the Maya Nord clearing. The second table (p. 73) presents the type and proportion of items eaten as well as the percent of feeding time for each item. This table includes a column stating percentage of feeding times for ingestion of soil, insects and edge plants (data that are a rare find). Table III (p. 74) contains information on the mineral composition of plants eaten and not eaten in the clearing and its immediate surrounding forest. The Magliocca and Gautier-Hion tables are especially valuable for the patterns that can be deduced on nutritional intake. Although some of the given information assists in decisions on type of flora, the tables do suffer from a familiar problem of being only fully meaningful if used by a researcher well versed in the characteristics of the species or one who has a second reference source that defines the species. Most important, however, is the authors' establishment of an overall nutritional/mineral

deficiency for the WLG in the dense THV of the surrounding marantaceae forest and the apparent significant role of the Maya Nord clearing in creating a sufficient mineral intake. The Marantaceae forests are relatively common in western Africa. No other research team appears to elaborate or examine the relationship of other food sources used to possible specific dietary deficiencies in THV and/or fruit items. Overall, this publication provides an important insight to the complexity of the interrelationship between habitat, diet and nutritional choice for the WLG populations.

Nouabale-Ndoki National Park, Republic of Congo

Blake, Stephen and Fay, Michael. 1997. Seed production by *Gilbertiodendron dewevrei* in Nouabale-Ndoki National Park, Congo, and its implication for large mammals. *Journal of Tropical Ecology* 12(6) 885-891.

This publication does not contain a tabulated format, but is an ecological investigation of one flora species (fruit) with emphasis on its value to a spectrum of fauna (including *Gorilla gorilla gorilla*) in the Nouabale-Ndoki National Park, Congo. The details include the life cycle of *Gilbertiodendron dewevrei* (also see Doran *et al.* below) and interaction with the local fauna at each stage of the *dewevrei* cycle. It is an insightful and distinctive article on how a flora's life cycle can affect that of indigenous fauna, i.e., an ecological relationship is systematically established. I concluded that this published research should be basic reading for those researching the ecology of a habitat, not necessarily for the information on the one species or one habitat region, but for a better understanding of the complexity of interactions and directionality within an ecological model.

Ndoki Forest of Nouabale-Ndoki National Park, Republic of Congo

Kuroda, Suehisa, Nishihara, Tomoaki, Suzuki, Sigeru, Oko, Rufin A. 1996. Sympatric chimpanzees and gorillas in the Ndoki Forest, Congo. In *Great Ape Societies*. (eds.) McGrew, W. C., Marchant L. F., Nishida, T. Cambridge University Press. pp.71-81.

Detailed tabulated food data are scant in the Kuroda *et al.* report. Table 6.1 (p. 73) contrasts the number and percentages of vegetation species eaten by the WLG gorilla and sympatric chimpanzees. The table also contrasts the number and percentages of items (fruit, seed, leaf, shoot with pith, stem bark and root, and flower) eaten by each of two species. Table

6.2 (p. 75) examines the nutritional content of major THV and AHV vegetation eaten. The seven items are listed by species. Because of the inclusion of AHV and that no chimpanzee-gorilla division was given, I assume this table reflected gorilla intake (chimpanzees do not frequent the swamps). Within the text, reference was made to a table 6.3 of which there was none (most likely an editing error). Textually, the species covered were quite limited in quantity as were the tables; however, for the flora species provided, they were well analyzed as to nutritional content. Doran *et al.* (see below) has greater quantity; Kuroda *et al.* offers greater detail on nutritional flora in the Nouabale-Ndoki National Park.

Mondika site at boundaries of Dzanga-Ndoki National Park, Central African Republic, and Republic of Congo

Doran, Diane M., McNeilage, Alistair, Greer, David, Bocian, Carolyn, Mehlman, Patrick, Shah, Natasha. 2002. Western Lowland gorilla diet and resource availability: New evidence, cross-site comparisons and reflections on indirect sampling methods. *American Journal of Primatology* 58: 91-116.

Doran and colleagues provide a table (p. 97) of stem densities of THV in forest types that results in an over-view of the various forest types at Mondika. On page 98 a second table takes the reader from forest types to the specific tree rations by stating, in decreasing percentage of total frequency, the 25 most common tree species at the site. The plant food (using family, species and local names) used by the WLGs is charted in table III (pp. 100-103). It includes flora parts consumed and how the samples were obtained, i.e., via following fresh gorilla trails to record use or by fecal collection and analysis. The latter type of collection was used to distinguish between male and female samples although there is some question as to the surety of such analysis. Much of these data were collected within Caesalpinaceae forests (*Gilbertiodendron dewevrei*), which extended the information by Blake and Fay (1997; see above) and gave further analysis on *Aframomum* (see Jones and Sabater Pi 1974). Table IV (p.6) noted in descending order (with percentages) important food species from trail sign data and included the form (herb, tree, insect, vine or shrub) and flora part eaten. The clarity of the information on how the data

samples were obtained and the life form designations in Table IV are valuable categories (and somewhat rare) for gorilla habitat/diet literature research.

Ndakan, Central African Republic and Mbeli Bai, Republic of Congo

Fay, J. M. 1997. The ecology, social organization, populations, habitat and history of the western lowland gorilla (*Gorilla gorilla gorilla*). Ph.D. thesis, Washington University, St. Louis, Missouri.

A main focus for Fay was forest vegetation and food availability at two sites in two countries. In summary Fay found that the lowland gorillas subsistence was leaves and stems of THV species of monocotyledons, leaves of the species of dicotyledons, fruit, seeds, bark and invertebrate foods. Tables 2.1-2.9 (pp. 33-38) provide details of dung analysis on dicotyledon fragments, monocot remains, *Aframomum* fiber, remains of THV and fruit found on feeding trails (also by season) and feeding trail remains other than THV or fruit (e.g., insects, bark or vine leaf). Table 2.10 (p. 39-41) lists gorilla food known in Ndakan by species (200 recorded) and by part (i.e., pulp, seed, leaf, etc.). In addition species themselves are discussed and described. Although this is a study with the limitations of indirect methodology, Fay's extensively discussed list from table 2.10 in itself could provide a basis for food species comparison with other sites.

Unfortunately few sites have such 'complete' (even indirect) surveys. Therefore, species not listed by other researchers on other sites may simply reflect the limits of the list, and not the absence of the species from the designated habitat. The Mbeli Bai site, forest types and families of flora are also thoroughly presented. In short, Fay's thesis is a fund of basic information on WLG diet in relation to species and flora type. It is not oriented toward nutritional evaluation as, for example, Magliocca and colleagues (1999, 2002, above), Remis *et al.* (2001, below) or Watts (1996, above).

Bai Hokou, Central African Republic

Goldsmith, Michele L. 1999a. Ecological constraints on the foraging effort of western gorillas (*Gorilla gorilla gorilla*) Bai Hokou, Central African Republic. *International Journal of Primatology* 20(1): 1-23.

Goldsmith finds that WLGs consume far more fruit in their diets than do MGs. As fruit is seasonal and clumped, the author examines the influence of the fruit intake on daily ranging

behavior. Goldsmith discusses availability and distribution of tree fruit, herb fruit and non-fruit vegetation. However, for the researcher seeking details regarding flora species and their dietary use by the WLG, the earlier study of M. Remis (1997b) as discussed below is more complete. As with many of the WLG studies indirect methods were used to gather data and these research gorilla populations were entirely unhabituated which creates questions on the accuracy of the daily ranges. However, Goldsmith does provide the researcher with sufficient information to conclude that fruit location and its seasonality are significant variables in determining ranging behavior.

Remis, Melissa J. 1997a. Ranging and grouping patterns of a western lowland gorilla group at Bai Hokou, Central African Republic. *American Journal of Primatology*. 43: 87-109.

The number of fruits in the diets of the three gorilla subspecies is tabled (p. 124) with ranging patterns (daily travel and annual home range) and each notation is identified with the appropriate study (researcher, date and length of project). Table II (p. 126) provides the same categories of information about chimpanzees and orangutans for comparative purposes. A primary objective of this study is to relate diet to grouping patterns, in particular, the flexibility (or not) of group cohesion. Remis' analysis speaks to subgrouping of some gorilla groups and the role not only of diet, but also the role of predation and infanticide risks. Remis' perspective elaborates the socio-ecological model and places diet in perspective in relation to that model.

Remis, Melissa J. 1997b. Western Lowland gorillas (*Gorilla gorilla gorilla*) as seasonal frugivores: use of variable resources. *American Journal of Primatology*. 43: 87-109.

In contrast to the MG, Remis argues that fruit eating and tree climbing are important to the WLG. To these ends, Remis documents the diet (including seasonality, and flexibility) of the gorillas at Bai Hokou. Table I (p. 91) gives food types, proportions of foods consumed during feeding bouts of males and females (separately) and intake differences between the wet and dry seasons. In Table III (p. 94) species of fruit found in fecal samples and selected fruits are graphed in more detail in relation to availability and consumption. Remis gives the researcher data on

fruit consumption, fallback foods, seasonality (with possible influence on ranging patterns) and the role of folivorous items in diet flexibility. There is also a repetition of the material in the previously discussed Remis 1997 paper (as above) on other diet research projects (i.e., researcher, date and length of project).

Remis M. J. 2000. Initial Studies on the contributions of body size and gastrointestinal passage rates to dietary flexibility among gorillas. *American Journal of Physical Anthropology*. 112: 171-180.

This study was conducted at the San Francisco Zoo on six WLGs and, therefore, was a controlled research project. The research was designed to increase understanding of the digestive physiology of the WLG (of which little is known) for clues as to whether seasonal dietary flexibility among gorillas corresponds to changes in digestive strategies and efficiency. Furthermore, the research provided preliminary insights into the physiological basis of food choice among gorillas. Remis discusses the findings in relation to field research on gorilla feeding ecology. Although the transference between captive and wild animal data is often (at best) tenuous, Remis awareness of the limitations is part of her discussion. Using directly observable methods in the field on forested WLGs who are minimally habituated to unhabituated has not been possible. Consequently, for research on the interrelationship of WLG habitat, diet and social systems Remis' detailed paper provides the basis for new questions and insights.

Remis, Melissa J., Dierenfeld, E. S., Mowry, C. B., Carroll, R. W. 2001. Nutritional aspects of western lowland gorilla (*Gorilla gorilla gorilla*) diet during seasons of fruit scarcity at Bai Hokou, Central African Republic. 22(5): 807-836.

Remis *et al.* analyze sixty-eight dietary plant samples for nutrients and other phytochemicals as well as differences in nutrients and phytochemicals between food categories (fruits and leaves), ripe and unripe fruit and important vs. less important foods (summary: Table II and III, p. 819-823). Remis and colleagues conclude that gorillas may be classified as frugivores/folivores with a diet that shifts along seasonal and interannual gradients at all low altitude sites and with high variability of amount of fleshy fruit. Such conclusions are consistent with the position that the digestive system of the gorilla is morphologically and physiologically

suiting to a diet that contains fruit (see Hladik *et al.*; Remis 2000; Taylor 2002). Such a perspective suggests that the MGs' almost entirely folivorous diet represents adjustment to an extreme *Gorilla* habitat (e.g., see Schaller 1963). The data and analysis are significant in relation to socio-ecological theory and a rationale for aspects (e.g., ranging patterns and foraging mechanisms) of social systems and possible differences among *Gorilla* subspecies.

Daja Faunal Reserve, Ntonga, (south central) Cameroon

Deblauwe, I., Dupain, J., Nguenang, G. M., Werdenich, D. and Van Elasacker, L. 2003.

Insectivory by *Gorilla gorilla gorilla* in southeastern Cameroon. *International Journal of Primatology* 24(3): 493-502.

Table I (p. 469) is a summary of the composition of the insect diet at the above WLG site and the frequencies of different insect prey in the WLG diet. Tables II, III and IV provide some cross-site comparison of several categories of insects (e.g., ants, termites, *Cubitermes sp*) within Belinga and Lope (Gabon), Ndoki (Congo), Dzanga-Sangha (Central African Republic) and Nionga (Cameroon). The indirect methods of fecal testing were used to determine insect intake (presence in feces [or not]) and the general frequency of ingestion. The majority of the article discusses insect food source within the Nionga site, consumption techniques and some nutritional detail. The gorilla locale in this article has little other published information. Furthermore, this is only article I located that dealt extensively with gorilla insectivory. The study had added value with the comparative information in relation to other sites. One obvious conclusion was that research on WLGs and insectivory is meager.

Lope Reserve, Gabon

Tutin, Caroline E. G., Williamson, Elizabeth A., Rogers, M. Elizabeth, Fernandez, Michel. 1991.

A case study of a plant-animal relationship: *Cola lizae* and lowland gorillas in the Lope Reserve, Gabon *Journal of Tropical Ecology* 7(2) 181-199.

The *Cola lizae* is a fruit bearing endemic tree (one of fifteen species in the *Cola* genus) that has a regular annual rhythm of production. The *Cola* dominates the Lope gorilla diet for four months each year, but it is the spatial distribution of the *Cola lizae* that has influence on the ranging patterns of the WLG. According to Tutin and colleagues, a mutualistic relationship exists

between the *Cola lizae* fruit and the gorilla. *Gorilla gorilla gorilla* is the only dispenser of the fruit species' seeds (no other species swallows the seed). Using *Cola lizae* as a guide, Tutin and colleagues take the reader on tour of the frugivory of the Lope WLG and the plant-animal relationship. Like the Blake/Fay study (above) the Tutin *et al.* presents an insightful investigation into the importance of ecological research. In particular it is evident that a specific examination of a flora/fauna interrelationship advances an understanding of role of those species within their habitat.

Lope Reserve, Gabon

Tutin, Caroline, Ham, Rebecca M., White, Lee J. T. and Harrison, Michael, J. S. Harrison. 1997.
The primate community of the Lope Reserve, Gabon: Diets, responses to fruit scarcity and effects on biomass.

Tutin *et al.* conducts a comparative dietary study of sympatric primate species, *Gorilla*, *Pan* and seven monkeys that reside on the Lope Reserve. The quantitative and qualitative analysis covers data collected over ten years. Habituation, especially of the WLG has proven an on-going problem. A disparity of methods and amounts of quantitative data gathered over different periods of time is acknowledged. Having noted these problems, Tutin *et al.* offer a series of tables (I-IV) to compare the percentage and number of flora species eaten, frequency of feeding within each food category, plant food dietary overlap and the keystone foods of the Lope primates. Lope has a low primate biomass and this study is an attempt to understand why. Tutin *et al.* present a possible historical-ecological explanation of the low primate biomass based on dietary keystones, vegetation history and a suggested dramatic environmental event (e.g., a climate change in past 25,000 years and/or a reduced forest cover as recently as 2,500 years ago). This study, then, is more than flora and fauna analysis, but is an integrated appraisal of the influence of biotic and abiotic processes and how they relate to the present environment. The researcher is given primary source data and an organized understanding of Lope as a habitat within a historical bioanthropological perspective.

Lope Reserve, Gabon

Tutin, Caroline and White, L. 1999. The recent evolutionary past of primate communities: Likely environmental impacts during the past three millennia. In *Primate Communities* (eds.) Fleagle, J. G., Janson, C. M. and Reed, K.E. Cambridge: Cambridge University Press. pp. 220-233.

Tutin and White have produced an evolutionary-historical overview on the variability of biomass, species and their interaction within the tropical African context and in relation to primate communities. Emphasized are the major vegetation changes in the Congo basin habitats. Phenological patterns, forest cover and biomass comparisons are examined. The material offered places the WLGs evolutionary adaptation in relation to flora in a comparative and developmental manner that provides a solid foundation in understanding the fullness of the ecological perspective. There are tables that summarize the pattern of use of fragmented forest habitat by members of the continuous forest primate communities at Lope and Kibale (p. 225) and state comparisons of biomass in forest and savanna ecotones in the Lope Reserve (as relate to Marantaceae forest and forest fragments). Moreover Tutin and White examine the structural and botanical differences between forest fragments and continuous forests that have major implications for primates in terms of food availability. This publication read in conjunction with Fay's 1997 (above) thesis provide the researcher with a substantial breadth of ecological (and flora) information.

EASTERN LOWLAND GORILLA

Kahuzi-Biefa National Park, (Zaire)

Yamagiwa, Juichi, Maruhashi, Tamake, Yumoto, Takakazu and Mwanza, Ndunda. 1996. Dietary and ranging overlap in sympatric gorillas and chimpanzees in Kahuzi-Biega National Park, Zaire. In *Great Ape Societies*: (eds.) McGrew, W. C., Marchant L. F., Nishida, T. Cambridge University Press. pp. 82-97.

In Table 2.2 (p. 88) dietary intake of plant forms (e.g., tree, vine, herb) and plant parts (e.g., fruit/seed, leaf) are compared between gorillas and chimpanzees (against a total number of flora species eaten jointly). Yamagiwa and colleagues compare the percentage of food items in various plant food species eaten by gorillas in four study areas (one MG, two WLG and ELG, Kahuzi site)(p. 83). The combining of fruit and seed into a category is unusual among

researchers, i.e., it is the flesh of fruit that is usually researched (however, see Tutin *et al.* 1991, above); consequently the four area comparisons are best accepted as preliminary and generalized. Watts (1996, see above), for example, isolates seeds as a category because of their ultimate fertilized reseeded of the habitat. Generally, Yamagiwa provides limited flora species specificity.

MISCELLANEOUS

Wrangham, Richard W. 1980. An ecological model of female-bonded groups. *Behaviour* 75: 262-299.

Within this seminal paper on the ecological model is an examination of a variety of primate species in relation to clumped (or not) food resource, i.e., density and distribution as a key to gregariousness. The relationship of food to female fitness and females to male fitness forms the underlying key to the why of certain grouping types, the later socio-ecological model and the rationale of why understanding habitat and diet are necessary (even if not sufficient). Therefore, although Wrangham's article is not a nutritional study in the sense of the above works, it is their fundamental rationale.

BRIEF DISCUSSION ON SELECTED ANNOTATED BIBLIOGRAPHY

1. Starting with entry one (Fossey 1983) a lack of consistency ensues as to which categories of food (e.g., lichens or roots) are used within the individual study. Cross comparisons of sites and studies that require such categories are therefore likely askew. Differences are also evident in how material is analyzed although, for example, Deblauwe's *et al.* (2003) study uses techniques and analytic methods chosen to be consistent with other sites.
2. The majority of the studies on the WLG use indirect methods of data collection on flora species for determining diet and percentages of intake of particular species (see chapter two of this thesis for analysis and comments on indirect method use with specific examples of studies). Direct methodology is more frequent in Karisoke research projects. This raises questions as to the comparability of results.

3. The operational length and apparent consistent record keeping of the Karisoke research station appear to create a unifying effect on data collection and a consistent accessibility for researchers to MG data. Such factors are absent in WLG studies (although there are some valiant attempts, e.g., Yamagiwa *et al.* 2003). Histories of established research sites and geography undoubtedly differ between the WLG and MG; hence, a created difference in data and research availability over time are apparent.