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RESEARCH ARTICLE

Impact of Ecological and Social Factors on Ranging in Western Gorillas

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We examined the influence of ecological (diet, swamp use, and rainfall) and social (intergroup interaction rate) factors on ranging behavior in one group of western gorillas (*Gorilla gorilla gorilla*) during a 16-month study. Relative to mountain gorillas, western gorillas live in habitats with reduced herb densities, more readily available fruit (from seasonal and rare fruit trees), and, at some sites, localized large open clearings (swamps and "bais"). Ranging behavior reflects these ecological differences. The daily path length (DPL) of western gorillas was longer (mean = 2,014 m) than that of mountain gorillas, and was largely related to fruit acquisition. Swamp use occurred frequently (27% of days) and incurred a 50% increase in DPL, and 77% of the variation in monthly frequency of swamp use was explained by ripe fruit availability within the swamp, and not by the absence of resources outside the swamp. The annual home-range size was 15.4 km^2. The western gorilla group foraged in larger areas each month, and reused them more frequently and consistently through time compared to mountain gorillas. In contrast to mountain gorillas, intergroup encounters occurred at least four times more frequently, were usually calm rather than aggressive, and had no consistent effect on DPL or monthly range size for one group of western gorillas. High genetic relatedness among at least some neighboring males [Bradley et al., Current Biology, in press] may help to explain these results, and raises intriguing questions about western gorilla social relationships. Am J Primatol 64:207–222, 2004. © 2004 Wiley-Liss, Inc.

Key words: western lowland gorillas; *Gorilla gorilla gorilla*; habitat use; frugivory; intergroup encounters

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INTRODUCTION

Many factors influence habitat use. These include intrinsic factors, such as body size and metabolic requirements [McNab, 1963; Milton & May, 1976; Nunn & Barton, 2000]; ecological factors, such as the density and distribution of food resources [reviewed in Chapman & Chapman, 2000; Watts, 2000]; and social and demographic factors, including mating strategies and group size and cohesion [Boinski & Garber, 2000; Isbell, 1990; Mitani & Rodman, 1979]. Variation in these factors across habitats and populations can lead to intraspecific variation in home-range size and habitat use (e.g., baboons [Barton et al., 1992], red howlers [Palacios & Rodriguez, 2001], orangutans [Singleton & van Schaik, 2001], and woolly monkeys [DiFiore, 2003]).

Gorillas (*Gorilla gorilla*) differ in ranging behavior across sites. Mountain (*G. g. beringei*) and eastern lowland (*G. g. graueri*) gorillas have relatively short (<1,000 m) daily path lengths (DPLs) [Achoka, 1993; Goldsmith, 2003; McNeilage, 2001; Schaller, 1963; Watts, 1996; Yamagiwa et al., 2003] and vary widely (4–40 km^2) in home-range size [Casimir, 1975; McNeilage, 2001; Robbins & McNeilage, 2003; Vedder, 1984; Watts, 1998a; Yamagiwa et al., 1996]. Much less is known about western gorilla ranging, because of the lack of habituated groups.

Gorilla ranging is best documented for Karisoke mountain gorillas, who feed primarily on abundant herbs and face little feeding competition, and as a result have short DPLs (500 m) and small (<2 km^2), intensely used monthly ranges [Fossey & Harcourt, 1977; Watts, 1996, 1998a]. Intensive foraging in what are essentially fields of herbs results in damaged plant stems and reduced profitability of an area. Gorillas move to new areas after a time, leading to continuously expanding home ranges, for periods as long as 7 years [Watts, 1998b, 2000]. Male–male competition has a strong (albeit short-term) effect on ranging [Watts, 1998b], and gorillas range farther on days of, or after, interactions with other groups or lone males [Watts, 1991]. Occasionally, dramatic home-range shifts will occur after several aggressive encounters with a male [Watts, 1998b]. However, over the long-term, responses to mating competition (for group males) are a "transient effect superimposed on the longer-term influence of food distribution" [Watts, 2000, p. 358].

Western gorillas (*G. g. gorilla*) live in tropical forests where herb densities are lower and fruit is more abundant compared to the high-altitude montane forests of mountain gorillas [reviewed in Doran & McNeilage, 1998, 2001]. Many, but not all, western gorilla habitats include localized, open clearings ("bais") covered with year-round herbaceous vegetation [Magliocca et al., 1999; Parnell, 2002], or large swamps bordering rivers [Blake et al., 1995; Fay et al., 1989; Nishihara, 1995; Williamson et al., 1988]. Western gorillas differ from mountain gorillas in diet and demography, in that they eat more fruit, live in groups of smaller maximum size (presumably as a result of increased feeding competition), and should potentially face higher male-mating competition when gorilla density is high and home-range overlap is great [Doran & McNeilage, 2001]. In previous studies we described western gorilla resource availability and diet at the Mondika Research Center [Doran et al., 2002] and provided genetic evidence of high gorilla density (>13 groups and two lone males) at the site [Bradley, 2003]. Here we examine the impact of these dietary and demographic differences on ranging. Previously, researchers found that western gorilla DPLs were two to five times longer than those of mountain gorillas, and increased with ripe fruit availability and consumption [Goldsmith, 1999; Tutin, 1996; Remis, 1997a]. These studies were based on data obtained by following trails of unhabituated gorillas (which are rarely attributable to specific groups), and relatively few complete DPLs. As a result, little is known about western gorilla home-range use (but see Cipolletta [2003] and Remis [1997a]), and it is unclear to what degree previously reported DPLs may have been inflated as a result of the gorillas being aware of and fleeing from the researchers trailing them [Cipolletta, 2003].

Here we report our findings regarding daily travel, home range, and swamp use of one partially habituated group of western gorillas that was followed on a daily basis.

First, we verify whether DPLs are longer in western gorillas compared to mountain gorillas, as one would predict on the basis of greater frugivory and decreased herb availability [Clutton-Brock & Harvey, 1977; Milton & May, 1976].

Second, we test which ecological and social factors best predict DPL by reexamining the dietary variables that were identified as key factors by Goldsmith [1999], as well as two additional variables: swamp use and intergroup interactions. We predict that daily travel should increase 1) with increasing fruit and decreasing leaf consumption (following Goldsmith [1999]); 2) after interactions with other groups or lone males, as in mountain gorillas [Watts, 1991]; and 3) when the swamp (which is located at the eastern edge of the study site) is visited.

Third, we consider why gorillas use swamps. Swamp use has been previously noted for eastern and western lowland gorillas (Kahuzi-Biega [Casimir, 1975], Lopé [Williamson et al., 1988], and Ndoki [Nishihara, 1995]). It has been hypothesized that aquatic herbs attract gorillas as a source of 1) carbohydrates during periods of fruit scarcity in terra firma forest [Magliocca & Gautier-Hion, 2002], 2) high-quality protein [Kuroda et al., 1996], or 3) minerals (particularly sodium [Nishihara, 1995]) throughout the year. We test whether swamp use is predictable at Mondika on the basis of the first two hypotheses. If this is so, swamp use should increase with decreasing terra firma fruit availability and/or decreasing terra firma *Haumania* shoot availability. In addition, since the swamp at Mondika includes forest that is inundated with fruiting trees as well as aquatic herbs, we test a fourth hypothesis: that swamp use is predictable on the basis of ripe fruit availability within the swamp, and gorillas travel to the swamp, at least at this site, primarily to feed on fruit rather than aquatic herbs.

Finally, we document home-range size. We examine whether western gorillas show a reduced tendency, compared to mountain gorillas, to expand their home-range size through time. This would be consistent with greater frugivory, since greater knowledge of resource location and spatial availability may be required for efficient frugivorous foraging [Milton, 1988].

MATERIALS AND METHODS

Study Site

Research was conducted at the Mondika Research Center (02° 21′ 859″ N, 016° 16′ 465″ E), located on the boundary of the Central African Republic (Dzanga-Ndoki National Park) and the Republic of Congo. The mean minimum and maximum daily temperatures averaged 21.0°C and 28.4°C ($n = 7$ years, July 1995–July 2002). The 50 km^2 study site consists primarily of a low-altitude (<400 m), mixed-species, semi-evergreen forest, with strips of monodominant *Gilbertiodendron dewevrei* (Caesalpiniaceae) forest along the Mondika stream, and swamp forest along the eastern edge of the study site. The site is free of human disturbance, has never been logged, and is rich in primate fauna.

Study Group

Data were obtained from April 2001 through July 2002, when we followed one group of gorillas, composed of 10 individuals (one adult silverback male, six adult females, and three infants). Contact was defined as time spent near (within short-range vocal communication distance), although not necessarily in direct sight of, gorillas, after we had vocally advertised our presence and heard a gorilla respond to us. We do not include data from the 2 years prior to April 2001, when we contacted the group frequently, because we could not always identify the group with certainty. After 8 April 2001 we followed the group on a near daily basis, contacted them frequently from the periphery of the group, and recognized the group silverback based on visual identification and his response to our presence (he frequently remained engaged in feeding or other activities). The gorillas were thus partially habituated to human observers, and the level of habituation continued to increase throughout the study period. Two measures indicate that our presence did not significantly increase gorilla DPL (see habituation results), as has been reported for gorillas that were unhabituated to human presence [Cipolletta, in press].

Methods and Analysis

Ranging behavior.

We calculated the DPL as the sum of distances (in meters) between consecutive Garmin GPS points (error $<10\,\text{m}$) recorded at each nest site, contact site, feeding tree visited, and change in travel direction for 334 complete nest-to-nest follows, for an average of 21 complete DPLs per month ($\text{SD}=3.3$, $\text{range}=13\text{–}26$, $n=16$ months). On average, 10.9 GPS points ($\text{SD}=4.0$, $\text{range}=3\text{–}26$) were used to calculate each DPL. For the home-range analysis, we included additional data from partial ($n=42$) and nearly complete follows ($n=77$), accounting for ranging behavior on 453 days or 95% of days during the study period. We drew each day's travel path onto a map of the study site, superimposed a $250\,\text{m}\times250\,\text{m}$ grid transparency, and recorded all quadrats entered during the day. We calculated the home range size as the number of different grids entered. We defined the core area as the minimum number of grids that accounted for 75% of the group's total entries.

Resource availability and diet.

We measured diet indirectly with both fecal samples and trail signs (presence/absence of food encountered along the trail) because viewing conditions prevented direct sampling of diet. We report only trail sign data because the two data sets provide largely overlapping and non-independent measures of diet. We previously determined that trail sign data are more accurate than fecal samples for describing the breadth of the diet, particularly, herb and leaf consumption, since it is impossible to identify these species macroscopically from fecal samples [Doran et al., 2002]. Each day we recorded the presence of each food item the first time we encountered it while following the group trail. Food items were recognizable by the characteristic manner in which they were processed, and by the particular plant parts discarded [Williamson, 1989]. Each day we tallied 1) the number of different species of fruit, leaf, and herb pith consumed to represent the variety of each food category in the diet (hereafter referred to as fruit, leaf, and herb); and 2) the total number of fruit trees visited per day, as a proxy for the total amount of fruit in the diet, hereafter referred to as number of fruit trees.

The strengths and weaknesses of these methods are detailed in Doran et al. [2002].

Swamp use.

We coded swamp use for each DPL as follows: 1) "complete swamp"—time spent entirely in the swamp, including morning and evening nest site; 2) "swamp use"—time spent partially in the swamp; and 3) "no swamp"–no time spent in the swamp.

Interactions.

We defined an interaction as "seeing or hearing another gorilla group or lone male when in contact or close proximity (usually $<100\,\text{m}$) with the focal group male." This is a more conservative definition than that used in mountain gorilla studies (groups within 500 m [Sicotte, 2001]), because of the more limited visibility at Mondika. We restricted analyses of rates of interactions to November 2001–October 2002, when we averaged $>100\,\text{hr}$ of contact time per month. The rates of interactions should be seen as minimal estimates due to the limited contact time.

Phenological monitoring.

Each month we monitored the presence or absence of 1) ripe fruit in 498 individuals of 57 species of trees and lianas that were previously determined to be important gorilla foods [Doran et al., 2002], and 2) new shoots of the most important gorilla herb, *Haumania danckelmaniana* (Maranthaceae), in 20 botanical plots placed along phenology trails.

Statistics.

We performed stepwise multiple regressions using SPSS version 11.5. Prior to the analyses, we evaluated variables for multicollinearity using SPSS tolerance measures, and no variables were so highly correlated that it would preclude their inclusion in the analyses. Stepwise regression was used to identify the subset of variables that would best predict the dependent variable. Variables were added sequentially, and the decision to add or remove a variable to or from the model was made automatically based on how much it changed multiple R^2. A variable was added if the change in R^2 was significant at the .05 level. Variables that were not entered into the model because they did not result in a significant increase in R^2 are referred to as excluded variables. Tests for significance were two-tailed.

RESULTS

Level of Habituation and Impact on Ranging

The total contact time was 1,569 hr, an average of 99 hr per month ($SD = 50$, $\text{range} = 59\text{–}190$, $n = 16$ months). Gorilla DPL did not increase significantly with human contact. This is indicated by the facts that 1) regression of the number of daily contacts with humans ($\text{mean} = 3$, $SD = 1.9$, $\text{range} = 0\text{–}7$, $n = 334$ days) on DPL had no significant effect on gorilla DPL ($F\,(1{,}330) = 1.1$, $P = .28$, $R^2 = .00$, adj. $R^2 = .00$), and 2) DPL did not decrease significantly through time, after the highly significant effects of fruit consumption and swamp use were controlled for (see below) (multiple regression of fruit consumption and a proxy for habituation (April 2001–July 2002 are numbered sequentially from 1–16) on non-swamp DPL:

standardized regression coefficient for habituation = .010, t = .177, $P = .859$, df = 2,239).

Resource Availability, Rainfall, and Diet

Rainfall was seasonal at the site with a 3-month dry season (December–February) characterized by <50 mm of rain per month (Fig. 1a). Rainfall was slightly higher (1,782 mm, n = 1 year) than average (mean = 1,577 mm; SD = 290; n = 6 years, 1996–2001; range = 1,085–1,818) during the study period. Fruit availability (Fig. 1b) was reduced relative to 2 prior years, particularly during June–September 2001, the usual major fruiting period (mean, SD, and n) for the present (April 2001–March 2002; individuals = (2%, 0%, 12), species = (11%, 0%, 12)) and previous years (individuals = (9%, 5%, 20), species = (38%, 18%, 20) [Doran et al., 2002]). Ripe fruit availability was significantly correlated with fruit consumption, inversely correlated with leaf consumption (although the latter was only a trend), and not significantly associated with herb consumption (Pearson r: fruit = 0.71, $P = 0.002$; leaf = –0.48, $P = 0.06$; herb = –0.374, $P = 0.15$; n = 16 months), as in all previous studies of gorilla diet, including those conducted at this site [Doran et al., 2002; Goldsmith, 1999].

DPL and Swamp Use

The mean DPL was 2,014 m (SD = 900, n = 334) with a considerable range (400–4,860 m). Gorillas visited the swamp on 27% of days, including 2.9% of days

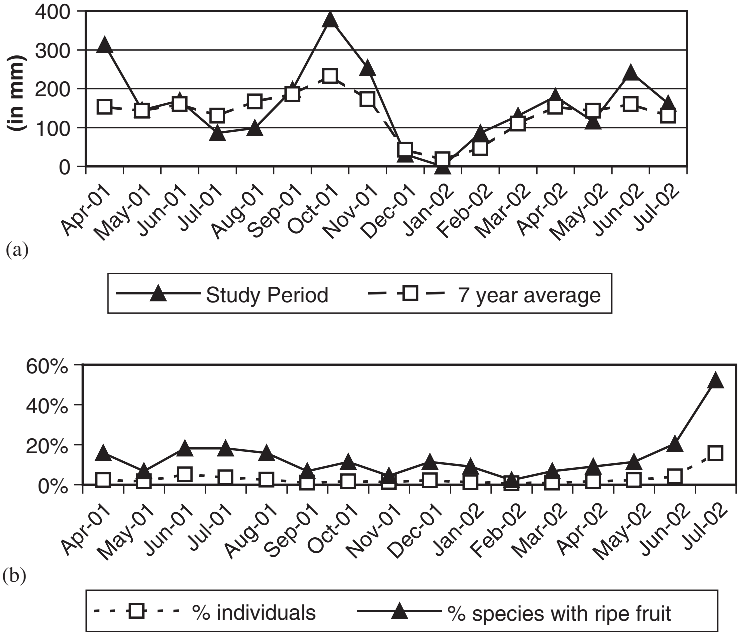

Fig. 1. Monthly variation in rainfall and resource availability, including (**a**) rainfall during the study period compared to average rainfall over 7 years, and (**b**) important gorilla fruit availability.

of complete swamp use (n = 449 total days for which swamp use was known, including complete and incomplete daily ranging).

To assess how ecological factors influenced overall DPL, we performed a stepwise multiple regression analysis of swamp use, rainfall, variety of herb, variety of leaf, variety of fruit, and amount of fruit in the diet on DPL. DPL increased significantly with the amount of fruit in diet and the frequency of swamp use. Together these two factors explained 49% of the variation in DPL (Table I). Two additional variables (herb and leaf) were also significant (herbs positively, and leaves negatively), but together they explained only an additional 1.5% of variation in DPL (Table IA). Rainfall and the variety of fruit were not significant and were thus excluded from the model.

DPL differed significantly with variation in swamp use (ANOVA: F(2,332) = 59.4, $P < 0.0001$). DPL was, on average, 53% longer on swamp vs. non-swamp days (mean DPL: swamp = 2,775, SD = 835, n = 80; non-swamp = 1,808, SD = 764, n = 247; complete swamp = 670, SD = 279, n = 8; all three pairwise comparisons were significant at $P < 0.05$).

We next considered whether different factors were associated with DPL on swamp and non-swamp days, excluding complete swamp days from analysis due to small sample size. We used a stepwise multiple regression analysis with the same independent variables listed above (minus swamp use) and regressed them on Non-Swamp DPL and Swamp DPL. Non-Swamp DPL increased significantly with the amount of fruit in the diet, and this factor explained 36% of the variation in Non-Swamp DPL (Table IB). The variety of fruit in the diet was also significant, but explained only an additional 3% of the variation. Swamp DPL also increased significantly with the amount of fruit in the diet, although this factor explained only 10% of the variation in DPL on swamp days (Table IC). Herb consumption was not significantly associated with swamp DPL.

TABLE I. Model Summary of a Stepwise Regression Analysis of Six Ecological Variables (Swamp Use, Rainfall, and Four Dietary Variables Including the Variety of Fruit, Herb, and Leaf Species in the Diet and the Amount of Fruit or Number of Fruit Trees Visited Per Day) on Gorilla Daily Path Length (Dependent Variable)*

	Variables included	R^2 change	F change	df	Sig. F change
A. All					
Model I	Fruit trees visited	.286	130.7	1,326	.000
Model II	I+swamp use	.210	135.6	1,325	.000
Model III	II+leaf	.006	3.9	1,324	.048
Model IV	III+herb	.009	5.9	1,323	0.16
B. Nonswamp					
Model I	Fruit trees visited	.362	135.9	1,239	.000
Model II	I+fruit	.028	10.8	1,238	.001
C. Swamp					
Model I	Fruit trees visited	.101	8.7	1,78	.004

*Dependent variables are daily path length for A: All days, B: Days with no ranging in swamp (nonswamp) and C: Days with ranging in swamp (swamp). Model I indicates the first variable to enter into the model. Model II indicates the second, etc. Values for R^2 change indicate how much the addition of each variable changes R^2.

Pattern of Swamp Use

The frequency of swamp use varied monthly (mean = 26% of days per month, SD = range = 0–77%, n = 16 months). We used a stepwise regression of independent variables (monthly terra firma forest availability of ripe fruit and herb shoots, rainfall, maximum temperature, and the presence of *Nauclea* sp. or *Grewia* sp. fruit in trail signs, a proxy for swamp fruit availability) that were predicted to influence the frequency of swamp use (dependent variable). All but one variable was excluded from the model. Ripe swamp fruit availability was significant, and explained 77% of the variation in the monthly frequency of swamp visits (adj. $R^2 = .789$, F (1,14) = 52.6, $P = 0.000$; Fig. 2). The frequency of swamp use did not increase with decreasing fruit or *Haumania* shoot availability outside the swamp, or with decreased rainfall or increased maximum daily temperature.

Relation of Social Factors to DPL

We recorded 48 interactions between the focal group and other groups or lone males, for an average of 4.0 per month (SD = 3.1, range = 0–9, n = 12 months). The focal group male response (recorded since June 2002) was variable, although ‘‘ignore’’ was the most common response (n: ignore = 8, flee/avoid = 7, aggression with or without physical contact = 1 and 3, respectively). We predicted an increasing frequency of interactions with other groups or solitary males with increasing frugivory (since the same fruit trees can be used by more than one group on the same day), swamp use (since these were localized and expected to draw several groups to them at the same time), and monthly home-range size (since more overlap with other groups would be expected). However, a model based on standard multiple regression of these variables on the frequency of interactions was not significant [F (3,12) = 0.394, $P = 0.759$]. The monthly frequency of interactions was not significantly related to DPL (mean monthly DPL and total number of interactions Pearson r = –0.10, $P = 0.70$, n = 16 months). The gorillas did not travel significantly farther after interactions: mean DPL did not differ significantly on days without (2,021 m, SD = 881, n = 301), with (1,878 m, SD = 964, n = 40), or immediately following (mean = 1915, SD = 810, n = 31) interactions (one-way between-subjects ANOVA F (2,369) = 0.61, $P = 0.54$).

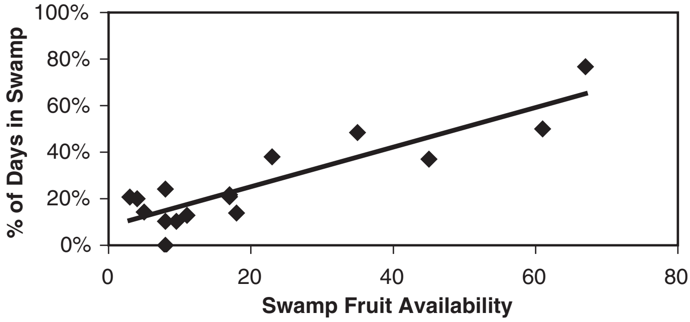

Fig. 2. Linear regression of monthly swamp fruit availability on the monthly frequency of swamp use. Adjusted $R^2 = 0.774$, $P = 0.000$, and n = 16 months.

Home-Range Size and Pattern of Use

The total home-range size for a period of 16 months was 15.75 km^2 (252 quadrats were entered, with no unvisited quadrats enclosed). It increased rapidly during the first 5 months and an asymptote was reached by 10 months (Fig. 3). The annual home-range size for the first 12 months of the study was 15.44 km^2. The group used a large part (41%) of their home range on a monthly basis. The mean monthly home-range size was 6.4 km^2 (SD = 1.3, range = 4.6–8.3 km^2, n = 16 months), and individual quadrats were entered frequently, although there was considerable variation (1–15 months) in frequency of use (average number of months entered = 6.5, SD = 4.4, n = 16 months; number of times entered = 15.5, SD = 14.9, range = 1–57, n = 252 quadrats). Forty-one percent of all quadrats (n = 252) were entered in at least half of all months, and 66% were entered in more than a quarter of the months sampled. The home-range core area was 5.62 km^2 or 36% of total home-range size. The core area was not contiguous, and included a block in the western, central, and eastern portions of the home range (Fig. 4).

We predicted that monthly home-range size (or area used each month) would increase with DPL, frugivory (since fruit is a rare and patchy resource), and swamp use (since the swamps are highly localized at one end of the gorillas home range), and we performed a stepwise multiple regression of these variables on monthly home-range size. All three factors were significant and together explained 71% of the variation in monthly home-range size (Table II). As predicted, the DPL and the area used each month were positively related. However, contrary to our predictions, ripe-fruit availability and frequency of swamp use were inversely related to monthly home-range size.

DISCUSSION

Ecological Influences on DPL

The dietary results reported here are consistent with those from an earlier 3-year diet study conducted at the same site [Doran et al., 2002]. With increasing fruit availability, gorillas ate more fruit and DPL increased, consistent with feeding on rare resources (17 of 22 species of important fruit trees occurred at

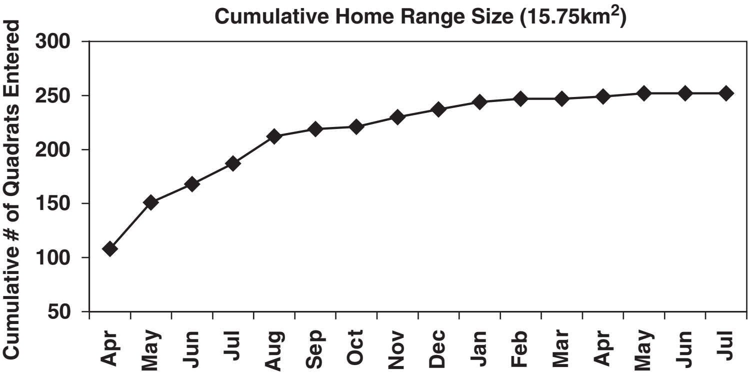

Fig. 3. Cumulative number of quadrats (250 m × 250 m) entered by one group of gorillas from April 2001–July 2002.

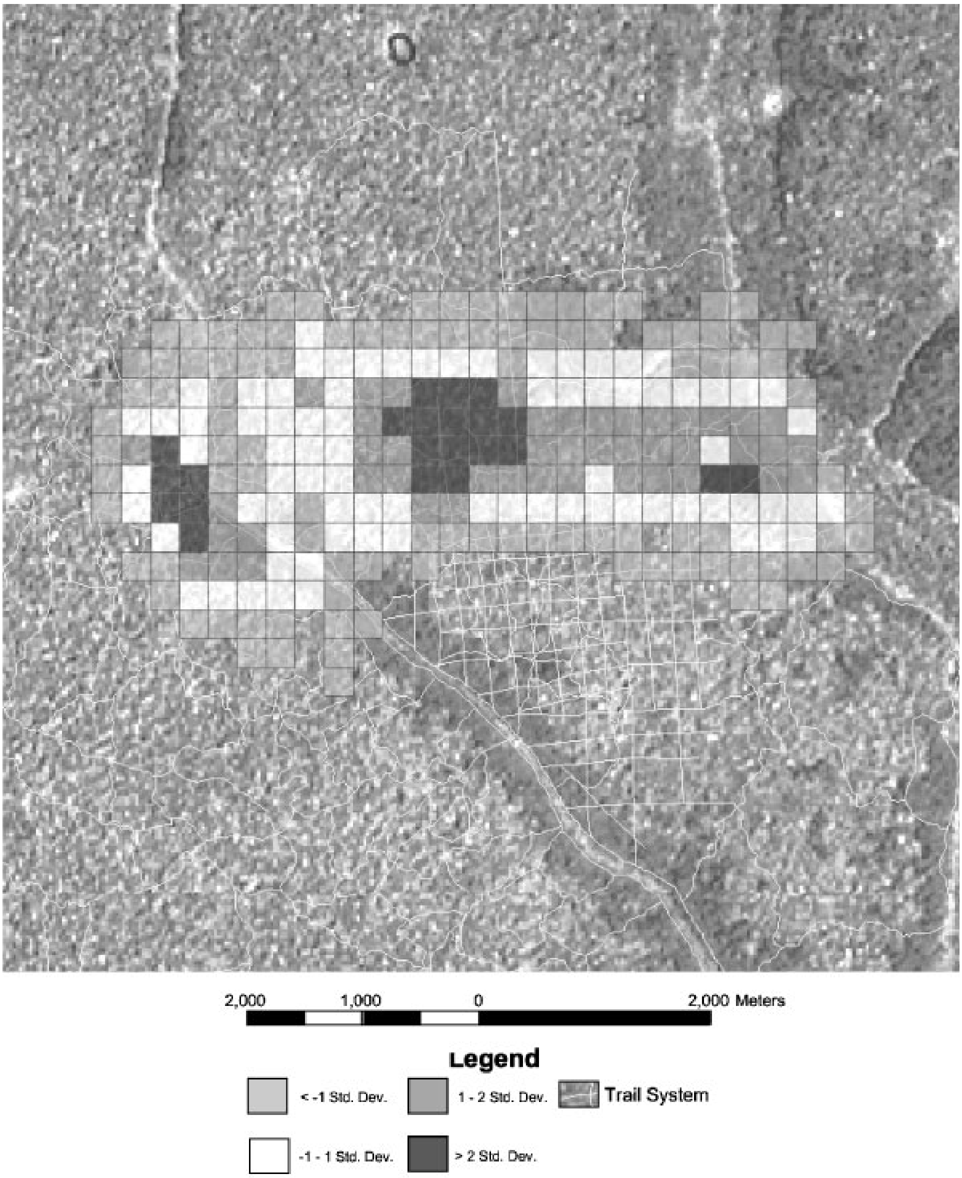

Fig. 4. Total home-range use by one focal group of western gorillas. Frequency of quadrat (250 × 250 m) use is indicated by shading. Darkest shading indicates that the quadrat was entered 2 SDs more frequently than the mean quadrat entrance. Swamp use occurs along the Ndoki River at the eastern end of the home range.

densities of <4 trees/ha [Doran et al., 2002]). When fruit availability decreased, the gorillas ate a wider variety of leaf species that were commonly available at the site [Doran et al., 2002], and DPL decreased. This energy-minimizing strategy is used by a variety of other primates during periods of reduced resource availability, including highly frugivorous woolly monkeys [DiFiore, 2003] and

TABLE II. Model Summary of a Stepwise Regression Analysis of Three Independent Variables (Daily Path Length or DPL, Amount of Fruit in the Diet, and Swamp Use) on Gorilla Monthly Range Size

	Variables included	R^2 change	F change	df	Sig. F change
Model I	DPL	.277	5.4	1,14	.036*
Model II	I+fruit	.266	7.6	1,13	.016*
Model III	II+swamp use	.226	11.8	1,12	.005**

Significant at $p < .05$(*) or $p < .01$(**).

chimpanzees [Doran, 1997], and folivorous species, such as sifakas, howlers, and siamangs [reviewed in Clutton-Brock, 1977].

Fruit consumption was the most important predictor of DPL. Nearly 50% of the variation in DPL was explained by the amount of fruit in the diet, as assessed by the number of fruit trees visited or the distance traveled to the swamp to access fruit. Even though fruit availability was particularly low during this study period, this finding is consistent with Goldsmith's [1999] previous results, and emphasizes the importance of ripe fruit in western gorilla foraging efforts.

The average non-swamp DPL was comparable to that observed by Cipolletta [2003] at Bai Hokou (where swamps are not present), and considerably shorter than those previously recorded at Bai Hokou by Remis [1997a] and Goldsmith [1999], suggesting that the early habituation process may lead to increased DPLs. Nevertheless, it is apparent that increased fruit consumption by western gorillas results in DPLs that are substantially (two to three times) longer than those observed in mountain gorillas.

Swamp Use

Gorillas used the swamp at Mondika to feed on both aquatic herbs and succulent fruit. Freshwater aquatic plants have been shown to contain higher mineral concentrations (especially sodium) relative to terrestrial plants in the area. It has been suggested that sodium hunger in gorillas is linked to feeding on aquatic plants [Kuroda et al., 1996; Magliocca & Gautier-Hion, 2002], as in other taxa (e.g., moose [Botkin et al., 1973], black and white Colobus monkeys [Oates, 1978], and barasingha [Moe, 1994]).

At other sites, gorillas visit ‘‘bais’’ regularly but infrequently (less than twice a month on average [Stokes, this issue]). While there, they spend virtually all their time feeding on aquatic herbs [Magliocca et al., 2002]. A novel finding of this study is the important role swamps, and particularly swamp fruit, may play in gorilla foraging strategy. At Mondika, gorillas also fed on a variety of aquatic herbs–most notably *Hydrocharis chevalieri*, which is relatively high in protein and sodium [Kuroda et al., 1996]. However ripe fruit, particularly two species of succulent fruit that were not available outside the swamp, appear to account for the much greater frequency of swamp use at the site. Swamps were not visited more frequently when ripe fruit or preferred herbs were less available in terra firma forest, as would be predicted if gorillas were seeking high-protein herbs or an additional carbohydrate source during periods of resource scarcity. Nor did the swamps appear to be used as a staple source of aquatic herbs, since they were used unevenly throughout the year. By traveling to the swamps, the gorillas incurred a substantial travel cost (50% greater than on non-swamp days). Nutritional data are not currently available to test the benefits of swamp use at Mondika, but future investigation will determine whether the particularly high sugar content of fruit, in addition to the higher mineral content of herbs, contributes to the swamp's great attraction for gorillas. Swamps are likely to provide a variety of resources that are not available elsewhere, and they may contribute to unusually high gorilla density in these areas, as reported for other swamp forests in the region [Fay, 1997; Fay & Agnagna, 1992].

Home-Range Use

The annual home-range size for the focal group was $15.4\,\mathrm{km}^2$, and a large portion was used on a monthly basis, as indicated by the large monthly range size and the fact that the current home-range size was reached quickly and remained stable throughout the study. This differs from mountain gorilla habitat use at Karisoke, where small areas were used on a monthly basis (monthly home-range size $= <2\,\mathrm{km}^2$) and home-range size increased steadily with time as the gorillas moved into new areas [Watts, 2000]. The differences in habitat use across sites are most likely related to differences in resource density and distribution. Herb densities were eight times higher at Karisoke relative to Mondika [Doran et al., 2002; Watts, 1984], allowing gorillas to use smaller areas intensively for the short term, with short daily-travel distances and small monthly ranges [Watts, 1998b, 2000]. At Mondika, herbs were both lower in density and more clumped in distribution than at Karisoke, with some species occurring in large discontinuous patches [Doran et al., 2002]. Given that fruits are even more rarely distributed than herbs, and the swamp is highly localized, it follows that gorillas must regularly forage in larger disparate areas in order to include each of these resources in their diet. The fact that home-range size did not continue to expand with time suggests that western gorilla home ranges are more stable through time than those of mountain gorillas, at least when the group male's tenure is not threatened by other males. This would be consistent with increased reliance on fruit, since more frequent use of the same areas is thought to confer benefits to fruit-eating primates (i.e., greater familiarity with an area, and travel along relatively fixed pathways may result in more efficient patterns of resource exploitation, including monitoring of important food resources [DiFiore, 2003; Oates, 1987]).

As predicted, the size of the area used each month increased with increasing daily travel. However, contrary to predictions, greater swamp use and frugivory, which were associated with longer DPLs, resulted in smaller monthly ranges. Increased frequency of swamp use may not lead to correspondingly larger monthly ranges as predicted, because although going to the swamp once increased monthly ranges (monthly range size was smallest in the 1 of 16 months the gorillas did not use the swamp), subsequent visits may not further range size because the gorillas frequently took similar paths into, through, and out of the swamp, and traveled to the swamp in a seemingly directed and rapid manner. Likewise, if some preferred fruit species are highly clumped in distribution, and revisited frequently throughout a month along similar paths, then the overall area used would not necessarily increase with increasing frugivory.

Home-range size should be predictable on the basis of habitat quality, population density, and degree of home-range overlap. At Mondika, gorilla density is relatively high, home-range overlap is great, DPL is long, and both monthly and annual home-range size is larger relative to that of a nearby western gorilla site (Bai Hokou). Given that terra firma herb densities are equivalent across sites, these differences appear to be largely attributable to the presence of the highly localized swamps at Mondika, which are absent at Bai Hokou.

Intergroup Interactions and Ranging

Interactions with other groups or lone males occurred a minimum of four times more frequently than for mountain gorillas at Karisoke (<1 per month [Sicotte, 2001]). Generally, intergroup interactions occur as a result of either mate or resource defense [Cheney, 1987]. In female dispersing species, including mountain gorillas, male mate defense is thought to play the major role [reviewed in Steenbeek, 1999]. The typical adult male mountain gorilla response to intruder males is aggression [Sicotte, 1993, 2001]. Groups travel farther on days after interactions, and may experience extreme range shifts as a result of serious (or potentially life-threatening) combat [Watts, 2000]. However, at Mondika, intergroup encounters did not have a consistent effect on the movements of one western gorilla group. The increased frequency of interactions did not generally lead to longer DPLs or larger monthly home ranges. The silverback's most frequent response to an outside male was to ignore him. Aggression, including aggression with physical contact, occurred, but infrequently compared to mountain gorillas. These findings are consistent with previous studies of western gorillas, which have documented both increased tolerance and occasional affiliative relationships between groups, including peaceful intermingling [Olejniczak, 1996] and co-nesting (Bermejo, this issue), as well as occasional extreme range shifts as a result of serious (or potentially life-threatening) combat (Cipolletta, this issue).

Varying levels of aggression toward outside males should be directly related to the perceived threat of a specific male, reflecting both the degree of vulnerability of the group male (his own age, physical condition, and number of females per group) and the relative familiarity of the intruder male [Cheney & Seyfarth, 1990; Kano, 1992; French et al., 1995; Stanford, 1991]. High genetic relatedness among at least some neighboring males [Bradley, 2003; Bradley et al., 2004] may help to explain the results, and raises intriguing questions about western gorilla social relationships.

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