

RESEARCH ARTICLE

Energetic Costs of Territorial Boundary Patrols by Wild Chimpanzees

SYLVIA J. AMSLER*

Department of Anthropology, University of Michigan, Ann Arbor, Michigan

Chimpanzees are well known for their territorial behavior. Males who belong to the same community routinely patrol their territories, occasionally making deep incursions into those of their neighbors. Male chimpanzees may obtain several fitness benefits by participating in territorial boundary patrols, but patrolling is also likely to involve fitness costs. Patrollers risk injury or even death, and patrols may be energetically costly and may involve opportunity costs. Although territorial patrols have been reported at all long-term chimpanzee study sites, quantitative data on their energetic costs have not previously been available. I evaluated the energy costs of patrolling for male chimpanzees at Ngogo, Kibale National Park, Uganda during 14 months of observation. In 29 patrols and matched control periods, I recorded the distances covered and time spent traveling and feeding by chimpanzees. I found that male chimpanzees covered longer distances, spent more time traveling, and spent less time feeding during patrols than during control periods. These results support the hypothesis that chimpanzees incur energetic costs while patrolling and suggest that ecological factors may constrain the ability of chimpanzees to patrol. *Am. J. Primatol.* 72:93–103, 2010. © 2009 Wiley-Liss, Inc.

Key words: chimpanzees; *Pan troglodytes*; territorial behavior; energetic costs; Kibale National Park

INTRODUCTION

Territorial animals defend an area against conspecifics [Burt, 1943; Noble, 1939]. In its most common form, displayed by many avian species, territorial defense involves one or both members of mated pairs defending areas associated with nests or reproductive activities [e.g. Hyman et al., 2004; Noble, 1939; Sergio & Newton, 2003; Stamps & Krishnan, 1999]. Less commonly, groups of animals compete over territories. Although group territoriality has been observed in several species of tropical birds [Gaston, 1978], it is comparatively rare among mammals, only having been reported in social carnivores [e.g. cheetahs: Caro & Collins, 1987; lions: Grinnell et al., 1995; spotted hyenas: Henschel & Skinner, 1991; Kruuk, 1972; wolves: Mech et al., 1998; Mech & Boitani, 2003; Packer et al., 2005; Schaller, 1972], and some species of primates [e.g. spider monkeys: Aureli et al., 2006; Wallace, 2008; bonnet macaques: Cooper et al., 2004; blue monkeys: Cords, 2007; white-faced capuchins: Crofoot, 2007; Gros-Louis et al., 2003; vervet monkeys: Struhsaker, 1967]. Chimpanzees provide one of the best examples of group territoriality in primates. Male chimpanzees of the same community jointly defend heavily used areas and routinely patrol peripheral areas in large parties, occasionally making deep incursions into the territories of their neighbors [Boesch & Boesch-Achermann, 2000; Goodall, 1986; Goodall et al., 1979; Herbinger et al., 2001; Mitani & Watts, 2005; Watts & Mitani, 2001; Wrangham, 1999].

During boundary patrols, chimpanzees appear to seek contact with or information about chimpanzees in adjacent communities. Behavior during patrols is characterized by the striking silence of males as they travel in a closely spaced, single-file line. Chimpanzees on patrol are particularly tense and attentive, move in a directed fashion, and engage in reassurance behavior when startled [Boesch & Boesch-Achermann, 2000; Goodall, 1986; Goodall et al., 1979; Mitani & Watts, 2005; Watts & Mitani, 2001].

Boundary patrolling is even rarer among mammals than group territoriality. Spotted hyenas, wolves, and spider monkeys are among the only other mammals to similarly patrol border regions and make incursions into the territories of neighboring groups [Aureli et al., 2006; Henschel & Skinner, 1991; Kruuk, 1972; Mech, 1994]. Although uncommon

Contract grant sponsors: National Science Foundation; University of Michigan Rackham Graduate School; the Little Rock Zoo; the Little Rock chapter of the American Association of Zookeepers; L.S.B. Leakey Foundation; National Science Foundation; Contract grant numbers: BCS-0215622; IOB-0516644.

*Correspondence to: Sylvia J. Amsler, 215 Crystal Court, Little Rock, AR 72205. E-mail: sjamsler@umich.edu

Received 10 February 2009; revised 15 September 2009; revision accepted 22 September 2009

DOI 10.1002/ajp.20757

Published online 27 October 2009 in Wiley InterScience (www.interscience.wiley.com).

in mammals, patrols occur universally at all chimpanzee study sites where multiple communities exist [Wilson et al., 2004; Wrangham, 1999].

Boundary patrolling may furnish several benefits to participants. Possible benefits include recruitment of females [Goodall et al., 1979; Mitani et al., 2002a; Nishida et al., 1985; Watts & Mitani, 2001; Watts et al., 2006; Wilson & Wrangham, 2003], resource defense [Williams et al., 2004], defense of the community against threats by outside males [Mitani & Watts, 2005; Mitani et al., 2002a; Watts & Mitani, 2001; Watts et al., 2006], elimination of rival males [Watts et al., 2006; Wilson & Wrangham, 2003], and a way for individuals to signal value as a cooperative partner to other males in the community [Watts & Mitani, 2001]. Evidence remains scant for many of these hypothesized benefits, though long-term data from Gombe strongly support the resource defense hypothesis, which posits that males patrol to maintain and increase territory size to provide better resources and thus improve reproduction by community members [Williams et al., 2004].

Despite these benefits, territorial boundary patrols are relatively infrequent, occurring at intervals of 10–23 days at various study sites [Boesch & Boesch-Achermann, 2000; Goodall, 1986; Mitani & Watts, 2005; Watts & Mitani, 2001]. The rarity of patrols suggests that the fitness benefits to participants are balanced by costs. Three potential costs include injury or death, opportunity costs, and energetic costs. First, there is an obvious potential risk of serious injury or death during intercommunity conflict. Lethal attacks are not uncommon during encounters between neighboring communities, and chimpanzees exhibit fear and hostility when they encounter members of neighboring communities [Wilson & Wrangham, 2003]. However, parties of males appear to reduce the risk of injury by modulating their willingness to engage neighbors based on relative party size [Boesch & Boesch-Achermann, 2000; Goodall, 1986; Goodall et al., 1979; Mitani & Watts, 2005; Watts & Mitani, 2001; Wilson et al., 2001, 2002]. By taking the offensive, patrollers are in a good position to assess power imbalances before initiating encounters, thereby minimizing such risks. Perhaps as a result of this advantage, males who participate in attacks rarely display obvious injuries [Watts et al., 2006].

Second, patrollers may also experience opportunity costs. The sometimes lengthy time spent on patrol is time that cannot be used to pursue other important activities, such as mating with estrous females. Female chimpanzees give birth only once every 5–6 years and exhibit few postpartum estrous cycles before conception [Boesch & Boesch-Achermann, 2000; Nishida et al., 2003; Sugiyama, 2004; Wallis, 1997]. Thus, males may suffer an opportunity cost in the form of lost matings by patrolling instead of following females who may be cycling in their own

community. Earlier research suggests that this potential cost does not reduce the probability that males will patrol [Mitani & Watts, 2005].

Energetic factors constitute a third cost associated with patrolling. Many discussions of patrols have assumed that energy costs constrain territorial activity [e.g. Herbinger et al., 2001; Mitani & Watts, 2005; Watts & Mitani, 2001; Wilson & Wrangham, 2003]. Patrolling chimpanzees engage in prolonged movements accompanied by little or no feeding [Boesch & Boesch-Achermann, 2000; Goodall et al., 1979; Mitani & Watts, 2005; Watts & Mitani, 2001]. Lengthy directed travel and losing chances to feed should increase the energetic costs of patrolling. The magnitude of these costs remains undetermined, however, as no quantitative measurement has been attempted.

In addition to the energetic effects of caloric intake and output through feeding and travel, travel rate may also contribute to the energetic cost of patrols. Because energy expenditure increases with increasing running speed in mammals independent of body mass, faster travel during patrols would exact an additional cost [Taylor et al., 1982]. All-male parties of spider monkeys, another primate species exhibiting fission–fusion sub-grouping and territorial boundary patrols, travel faster when in boundary areas than at other times [Shimooka, 2005].

Despite the widespread occurrence of patrolling behavior by chimpanzees, quantitative data on the energetic costs of patrols do not exist [Mitani et al., 2002a; Watts & Mitani, 2001]. In this article, I investigate these costs using observations of travel and feeding during patrols and comparing them with similar observations made on control days when patrols did not take place. I predicted that patrolling chimpanzees feed less, travel more, cover more distance, and travel faster than they do when not on patrol. In addition, using published values for chimpanzee energy expenditure during locomotion [Sockol et al., 2007], I hypothesized that patrolling significantly increases transport costs compared with normal daily travel.

METHODS

Study Site and Subjects

I collected behavioral observations of chimpanzees during 14 months of fieldwork in 2004–2006 at Ngogo, Kibale National Park, Uganda. The site is covered primarily by tall, moist evergreen forest, with areas of swamp, grassland, woodland thicket, and colonizing forest. Struhsaker [1997] provides a detailed description of the study area. Ngogo has been the site of behavioral research on several primate species (*ibid*), and chimpanzees there have been observed continuously since 1995 [Mitani, 2006; Mitani et al., 2000, 2002a,b; Watts et al., 2006]. As a result, the chimpanzees of Ngogo are habituated to

and individually identifiable by human observers. Approximately 230 km of trails cover the $\sim 30 \text{ km}^2$ Ngogo study area. I used a handheld GPS to map the entire trail system. I mapped trails by connecting points taken at trail intersections and wherever trails deviate from a straight north–south or east–west path. The resulting map facilitated plotting the locations of chimpanzees.

The Ngogo chimpanzee community is the largest described in the wild and includes many males [Mitani, 2006; Mitani & Amsler, 2003; Watts, 2000a,b, 2002, 2004; Watts & Mitani, 2000, 2001; Watts et al., 2006]. Community size ranged from 137 to 148 individuals with 26–29 adult males over the course of this study.

Behavioral Observations

Data collection was noninvasive and approved by the University Committee on Use and Care of Animals at the University of Michigan. I conducted this research with the permission of the Uganda Wildlife Authority and the Uganda National Council for Science and Technology.

I recorded four variables to determine the energetic costs of patrols: (1) the proportion of time spent traveling; (2) the proportion of time spent feeding; (3) distance covered, controlling for observation time, and (4) travel rate, measured as the distance covered per unit travel time. I recorded these data during patrols and during control observations.

I located chimpanzee parties each day by checking food trees, listening for calls, walking the trail system, or returning to individuals followed the previous day. Once chimpanzees were located, I conducted 2 hr focal animal samples of adult males, continuously recording data on their feeding behavior and travel. I selected focal subjects on a pseudorandom basis, with priority given to those individuals who had been sampled infrequently.

For each feeding and travel bout by a focal male, I recorded the start and end time to within 1 min. These periods of time were summed across the observation time to yield the time spent feeding and time spent traveling. I also took geographic coordinates with a Magellan 315 GPS receiver. When the unit was locked into satellites, I recorded GPS readings at the start of travel, every 2 min during travel, and when travel stopped or paused. When the unit could not track enough satellites to obtain a fix, I noted trails and the times they were crossed. In these cases, I estimated the direction and distance in meters from known locations or previous GPS readings. I used the coordinates to create travel paths for patrols and focal follows.

I also conducted scan samples at 30 min sample intervals, during which I noted individuals in the party. I defined parties as all individuals present and within visual range of other chimpanzees, as

assessed by observers [Mitani & Amsler, 2003; Pepper et al., 1999; Wakefield, 2008].

Observations during patrols

Patrols are easily recognizable. Patrolling chimpanzees move toward and along borders, and sometimes travel into the territories of others. Patrols also involve a distinctive set of behaviors. Patrolers are unusually quiet, maintain close proximity, and travel in single file. They pause frequently and are unusually alert and attentive to their surroundings. Patrolling chimpanzees sometimes stand bipedally or climb trees to scan the area. They frequently sniff the ground and vegetation, and inspect any signs of chimpanzees that they find, such as nests, food wadges, or feces [Boesch & Boesch-Achermann, 2000; Goodall, 1986; Goodall et al., 1979; Mitani & Watts, 2005; Watts & Mitani, 2001].

To test my four predictions, I calculated the time spent traveling and feeding during patrols, the distance traveled on complete patrol paths, and travel rates. During patrols, I typically followed chimpanzees as they moved in a single-file line. Thus, when foliage was dense or the patrol party was particularly large, I could constantly observe only the behavior of individuals toward the back of the line. Because males closely coordinate their behavior during patrols, start and stop travel times usually applied to all individuals, so I could continue focal animal samples even when my view of the focal individual was obscured by others. I recorded ad libitum feeding by any visible participant rather than just focal subjects, which likely inflates the feeding time above that of focal animals. This measure thus represents a conservative choice for comparison with control observations. I divided the time spent feeding and traveling by the total time, resulting in proportions of time spent feeding and traveling. To correct for unequal observation times, I also divided the distance traveled by the total time spent on patrol (total time includes both travel time and patrol time that was not spent traveling). To determine travel rates, I calculated the distance covered per unit of travel time only. To match patrols to control observations, I also recorded the number of participating males.

I recorded complete patrol paths and travel times, which included both the trip out and the return. I defined the start time of the patrol as the moment chimpanzees first began to exhibit distinctive patrol behavior, including silence, cohesive and directed travel, frequent attentive pauses, and sniffing of the ground, vegetation, or signs of chimpanzees [Boesch & Boesch-Achermann, 2000; Goodall, 1986; Goodall et al., 1979; Mitani & Watts, 2005; Watts & Mitani, 2001]. For many patrols the start time was clear because a cohesive party of mostly male chimpanzees quickly formed. In these cases,

males abruptly and simultaneously stopped feeding or resting and jumped up and quickly moved off together, sometimes separating from females and their young as they did so. This sudden gathering and movement was generally accompanied by fear grimaces and embracing among party members. It was occasionally precipitated by distant calls from a neighboring group. For other patrols, chimpanzees were already traveling, making it more difficult to identify start times. In these cases, I defined start times of patrols in one of two ways, after (1) the last audible call was uttered or (2) most females dropped out of the party.

I considered patrols to continue until the Ngogo chimpanzees returned to their territory and either made considerable noise by calling loudly and displaying, including buttress drumming displays, or simply resumed normal calling behavior. When patrollers did not meet neighbors or only made auditory contact with them, they generally remained cohesive as they returned to the Ngogo territory. In these situations, chimpanzees called and displayed once they returned to their territory, and I could record observations that applied to all patrol participants. When patrolling individuals encountered other chimpanzees, however, patrollers often scattered and moved back rapidly to the Ngogo territory in smaller parties that traveled in parallel. In these cases, I followed one of the subgroups, and continued noting the patrol path and events for those individuals only.

I also collected data ad libitum on events during patrols. Events included the following: sniffing the ground, vegetation, nests, feces, or other signs of chimpanzees from neighboring communities; unusually tense or alert behavior; fear grins; embraces between patrol members; calls, most notably screams and whimpers; reactions to hearing chimpanzees from other communities; displays and drumming; battles, consisting of visual contact, confrontation, charges, and chases between Ngogo patrollers and members of the opposing party; attacks on other chimpanzees; infanticides; consumption of killed infants; and any other distinctive or unusual behavior.

Control observations

I compared observations of patrolling behavior with control observations. Controls included focal animal samples of adult males that I collected on days that chimpanzees did not patrol. I used a matched-pairs design to compare behavior during patrols with control observations. I selected controls that occurred within a period that started 10 days before a patrol and ended 10 days after it (mean difference = 5.7 days, SD = 2.6, range = 1–10, $n = 29$ pairs). Controls were also matched to patrols with respect to time of day and the number of males in the party. In this way, I attempted to control for the

effects of food availability, time of day, and party size on travel. Because all control follows were 2 hr while patrols varied in length, I used the midpoint times of control periods and of patrols to match time of day (mean difference = 54 min, SD = 62, range = 0–280, $n = 29$ pairs). Party scans were taken every half an hour during each control follow and patrol, and I used the maximum number of males present during scans for each control period and patrol to match the number of males in parties (mean difference = 1.9 males, SD = 2.0, range = 0–9, $n = 29$ pairs). To ensure that male numbers did not account for differences in travel and feeding, I selected two additional sets of control observations matched closely on the maximum and average number of males present during scans, and loosened the food availability and time of day criteria. I confirmed results by conducting analyses on these complementary sets of matched pairs.

For each 2 hr control sample, I determined the time the focal individual spent traveling and feeding. To control for unequal observation times, I divided these by the observation time of 2 hr, resulting in proportion of time spent traveling and feeding. I also calculated the distance covered on travel paths of focal samples. As I did with patrols, I divided this distance by the total number of minutes in the focal follow. I determined travel rates based on the distance covered during travel only.

Cost of Transport

I calculated energy expenditure during patrols and control observations using distances traveled and published values for the cost of transport in chimpanzees. Sockol et al. [2007] calculated the cost of quadrupedal walking for adult male chimpanzees to be 0.19 ml O₂ per kg of body weight per meter moved. I converted this value to energy expenditure expressed in kilocalories (kcal) based on the assumption that consumption of a liter of O₂ corresponds to about 4.83 kcal of energy [Campbell et al., 1999]. I estimated adult male body mass at 42.7 kg, a value derived from 21 wild shot East African chimpanzees (*Pan troglodytes schweinfurthii*) [Smith & Jungers, 1997]. This value may underestimate the weight of male chimpanzees in the Kibale National Park, which has been estimated at 45–55 kg based on skeletal measurements of the remains of three individuals [Kerbis Peterhans et al., 1993]. I nevertheless use the lower figure because it is based on a larger sample of individuals of known body mass [cf. Pontzer & Wrangham, 2004].

I also estimated the daily cost of transport for adult male chimpanzees at Ngogo. I calculated the average distance traveled per hour for all focal observations of at least 2 hr that occurred on days that the chimpanzees did not patrol. Focal observations were distributed fairly evenly through the day, though I conducted fewer toward the end of the day,

TABLE I. Distribution and Mean Travel Distances of Focal Observations Across the Day

Start time of focal observation	# of focal observations	Mean travel distance (m)*
7:01–8:00	49	604
8:01–9:00	59	512
9:01–10:00	54	522
10:01–11:00	67	562
11:01–12:00	50	601
12:01–13:00	46	594
13:01–14:00	57	710
14:01–15:00	35	635
15:01–16:00	33	718
16:01–17:00	2	787

*Calculated for 2 hr focal samples.

while the mean distance traveled over a 2 hr period increased gradually through the day (Table I). I estimated daily transport costs by calculating kcal consumption per hour based on the average hourly travel distance and multiplying that value by 12 hr. Using the distances covered on the 29 patrol paths, I also determined the cost of transport for each patrol. I subtracted the time spent on each patrol from 12 hr, and multiplied the remaining number of hours in the day by the average hourly transport cost for nonpatrol days. This provided an estimate for energy expenditure during the part of the day that the chimpanzees did not patrol. I added this figure to the cost of transport for the patrol to obtain a value of the total cost of transport for each day that the chimpanzees patrolled.

Statistical Analysis

For each patrol and matched control I calculated the proportion of time spent traveling, the proportion of time spent feeding, the distance covered per unit observation time, and the actual travel rate (= distance covered/time spent traveling). I plotted the distribution of values of each variable separately for patrols and control periods. Values were not normally distributed, and I used the nonparametric Wilcoxon signed-rank test to examine whether variables differed between patrol and control conditions. I performed a *t*-test to assess whether chimpanzees increase their daily transport costs by patrolling. I compared the mean of the sample of daily transport costs for the 29 patrol days with the estimated daily transport cost for days on which the chimpanzees did not patrol.

Other researchers recorded data on patrols that are included in these analyses. In the cases where I was not present at a patrol ($n = 8$), some data were not collected. Patrols without sufficient data for any given variable were eliminated, resulting in differences in sample sizes among the following

analyses. I performed all statistical tests using SAS release 9.1.3.

Equal Observation Times

In the analyses described above, I accounted for unequal observation times within pairs by dividing travel time, feeding time, and distance by the total observation time. I also conducted complementary analyses, for which I randomly selected a window of time from the longer observation in each pair to match the length of time of the shorter observation. I truncated the patrol time to match the 2 hr focal sample in 16 pairs, and truncated the control sample to match the shorter patrol in 13 pairs. This process resulted in equal observation times within pairs. I verified the results of the analyses above by comparing travel time, feeding time, travel distance, and travel rate on these time-standardized samples using Wilcoxon signed-rank tests.

RESULTS

I collected observations of feeding and travel during 29 boundary patrols. Figure 1a shows the travel paths for these patrols. I recorded data on distances covered for 29 patrols, on the proportions of time spent traveling and travel rates for 25 patrols, and on the proportions of time spent feeding for 23 patrols (Table II).

Behavior During Patrols

Patrollers usually started out moving quickly and in a directed fashion, sometimes pausing after a few minutes to wait for stragglers to catch up. After this initial rapid travel, they usually interspersed longer travel bouts with shorter rest bouts, apparently listening for other chimpanzees during pauses. Patrolling chimpanzees often stopped on ridges, where calls and other sounds made by conspecifics can be heard over long distances. They also stopped to sniff vegetation or signs of chimpanzees. When patrollers heard other chimpanzees, they excitedly embraced each other, fear-grimaced, and sometimes uttered low amplitude screams that did not carry far before moving quickly in the direction of the calls.

Return trips generally involved more continuous and directed travel than trips out, especially in cases where patrollers made deep incursions into the territories of neighbors. For 12 patrols that had a clear turnaround point, patrol parties spent significantly more time traveling (Wilcoxon signed-rank test, $T = 33$, $P < 0.001$) and covered significantly greater distances (Wilcoxon signed-rank test, $T = 39$, $P < 0.0005$) before they turned around than they did during the return trip. When patrollers met one or few females and committed an infanticide, they tended to stay in the area for an hour or more before traveling back to the Ngogo territory. If they met a

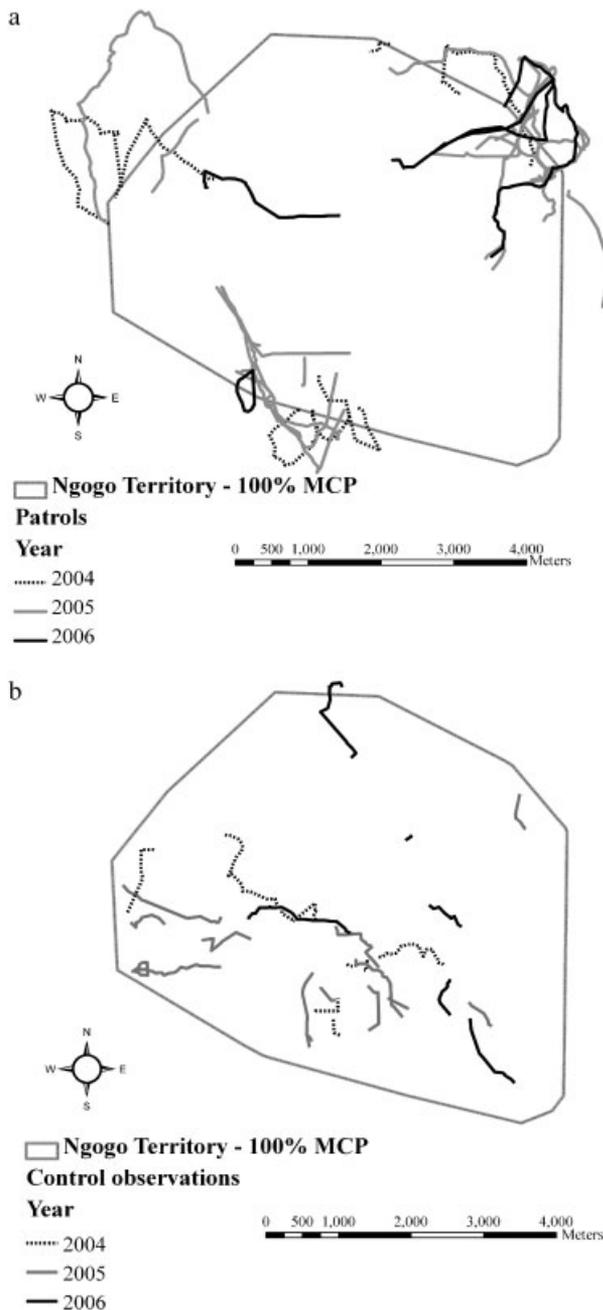


Fig. 1. Maps showing the paths followed during patrols (a) and control periods (b).

large group from another community, the encounter was generally over within 25 min, followed by direct and rapid travel back to the Ngogo territory.

Travel Costs

Patrols lasted an average of 134 min, varying from 15 to 348 min (SD = 88 min, $n = 29$). Chimpanzees traveled more than half the time on average while on patrol (mean = 58%; SD = 21%; range: 25–100%; $n = 25$ patrols). In contrast, during control periods they

spent only about 14% of their time traveling (SD = 9%; range: 0–35%; $n = 25$ controls). Thus, chimpanzees spent significantly more time traveling during patrols than they did during control periods (Wilcoxon signed-rank test, $T = 163$, $P < 0.0001$; Fig. 2).

Because chimpanzees spent considerable time traveling during patrols, patrollers were likely to cover long distances. In fact, travel distances during patrols ranged from short (c. 0.5 km) “checks” near border areas to much longer treks of more than 5 km (mean = 2456 m; SD = 1492 m, $n = 29$; Table II; Fig. 1a). These distances were longer than those covered during 2 hr control periods, correcting for observation time (Wilcoxon signed-rank test, $T = 216.5$, $P < 0.0001$; Fig. 3). Patrollers moved a mean distance of 21 m per minute of observation time (SD = 9; range: 7–48; $n = 29$ patrols). In contrast, the mean distance covered during control periods was only 6 m per minute of observation time (SD = 4; range: 0–14; $n = 29$ controls).

Based on the distances covered, adult male chimpanzees consumed an estimated 0.81 kcal per minute during patrols (SD = 0.34; range = 0.26–1.89; $n = 29$ patrols), compared with 0.24 kcal per minute during control observations (SD = 0.15; range: 0–0.54 kcal; $n = 29$ controls). In 452 focal observations of at least 2 hr that occurred on days that the chimpanzees did not patrol, the average distance traveled per hour was 302 m (SD = 260; range: 0–1608 m; $n = 452$), which requires consumption of 11.82 kcal (SD = 10.20; range: 0–63.0 kcal; $n = 452$). In a 12 hr day this translates to 141.84 kcal consumed to support transport costs. Chimpanzees expended an average of 96.25 kcal per patrol (SD = 58.48; range: 15.95–214.82 kcal; $n = 29$ patrols). Their average estimated total daily transport cost for patrol days was 194.62 kcal (SD = 45.24; range: 150.57–300.49 kcal; $n = 29$ patrol days), which was significantly greater than the usual 141.84 kcal expended on a day without patrolling activity (t -test, $t = 8.33$, $P < 0.0001$).

Despite traveling long distances during patrols, the mean travel rate, computed as the distance traveled per unit travel time, was actually faster during control periods (44 m/min; SD = 18; range: 0–94; $n = 25$ controls) than patrols (36 m/min; SD = 7; range: 25–51; $n = 25$ patrols). This difference was significant Wilcoxon signed-rank test, $T = 80.5$, $P < 0.05$; Fig. 3) and indicated that chimpanzees traveled slower but more steadily while on patrol than other times.

Feeding Costs

I rarely observed feeding by patrolling chimpanzees. Patrollers occasionally fed on one or two fallen fruits as they paused to sniff broken branches and vegetation under food trees in a neighbor’s territory. In these cases, only one or two individuals typically fed. During other times, chimpanzees ate the leaves

TABLE II. Observations of Patrols by Chimpanzees at Ngogo

Date M/D/Y	Total time (min)	Proportion of time spent traveling	Proportion of time spent feeding	Distance (m)	Distance covered (per unit patrol time—m/min)	Travel rate (m/min)	Party size	# of males
8/1/04	164	0.50	0	3,318	20.23	40.46	12	11
8/6/04	47	No data	No data	2,271	48.32	No data	15	15
9/14/04	15	1.00	0	428	28.53	28.53	12	12
10/5/04	45	No data	No data	1,057	23.49	No data	20	20
10/6/04	198	0.36	0.30	2,147	10.84	29.82	32	27
10/12/04	322	0.43	0	3,918	12.17	28.09	28	27
11/9/04	185	0.45	0.44	2,582	13.96	30.92	32	29
2/12/05	38	0.95	0	932	24.53	25.89	20	18
2/18/05	82	0.66	No data	2,352	28.68	43.56	16	15
2/21/05	170	0.75	0.01	4,547	26.75	35.66	20	20
2/22/05	165	No data	No data	1,813	10.99	No data	10	10
2/28/05	43	0.51	0	994	23.12	45.18	20	19
3/2/05	264	0.64	0.003	5,374	20.36	31.89	20	19
3/10/05	155	0.85	0	3,878	25.02	29.38	16	16
3/25/05	49	0.85	No data	1,482	30.24	35.71	12	10
4/13/05	84	0.71	0.04	2,360	28.10	39.66	20	19
4/13/05	47	0.49	0	567	12.06	24.65	11	10
4/23/05	86	0.64	0	2,304	26.79	41.89	14	12
4/23/05	173	0.51	0.02	2,746	15.87	30.85	12	12
5/4/05	70	0.81	0	1,944	27.77	34.11	19	17
10/12/05	137	0.30	0.09	1,274	9.30	30.70	19	18
10/13/05	125	0.62	0.33	3,096	24.77	39.95	25	23
12/27/05	36	0.25	0	407	11.31	45.22	21	18
12/28/05	348	0.42	0.28	5,482	15.75	37.81	23	23
1/23/06	266	0.52	0.29	5,020	18.87	36.38	15	14
1/30/06	164	0.28	0	2,375	14.48	51.08	11	10
2/1/06	181	0.66	0.39	4,270	23.59	35.88	9	9
2/3/06	86	0.41	0	1,396	16.23	39.32	20	20
2/5/06	135	No data	No data	899	6.66	No data	14	14

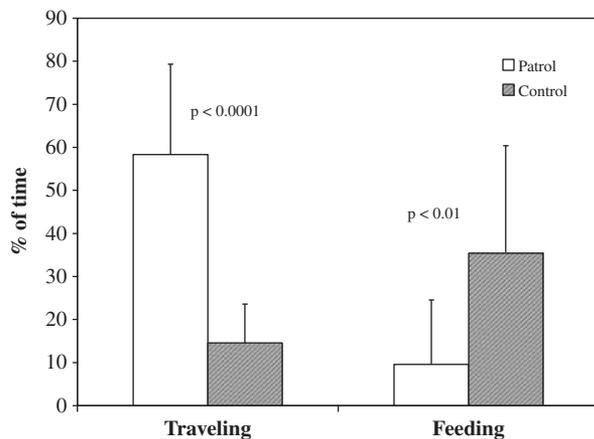


Fig. 2. Comparison of the average time spent traveling and feeding during patrols and control periods. Means+1 SD are displayed.

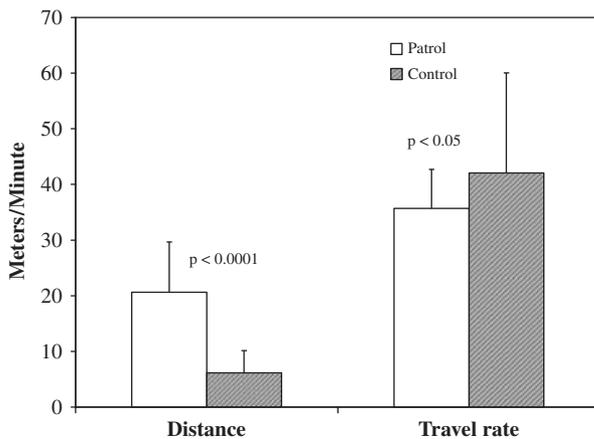


Fig. 3. Comparison of distance covered and travel rate during patrols and control periods. Distance is calculated as the meters covered per minute of observation time. Travel rate is the actual travel rate expressed in meters covered per minute of travel time. Means+1 SD are displayed.

of saplings while pausing, often on a ridge, apparently listening for other chimpanzees.

I recorded sustained feeding bouts during patrols in only two contexts. Three times patrolling chimpanzees encountered and hunted red colobus or black and white colobus monkeys that they subsequently consumed. Twice patrollers killed and consumed infant chimpanzees from other communities, and those in possession of dead infants fed on them for a long time. Following one of these infanticides, several chimpanzees fed on the ripe fruit of *Morus mesozygia* for almost an hour and a half while one male cannibalized the infant.

Excluding these five patrols, chimpanzees spent only about 3% of their time feeding during patrols (mean = 2.7%; SD = 7.9%; range: 0–32.8%; $n = 19$ patrols). In contrast, they spent 40% of their time feeding during matched control periods (SD = 23.6%;

range: 0–82.5%; $n = 19$ controls). Chimpanzees thus spent significantly less time feeding during patrols than during control periods (Wilcoxon signed-rank test, $T = 74.5$, $P < 0.0001$).

Including the five exceptional cases had no appreciable effect on the preceding analysis as chimpanzees still spent significantly less time feeding during patrols than during control periods (Wilcoxon signed-rank test, $T = 83.5$, $P < 0.01$; Fig. 2). Chimpanzees spent less than 10% of their time feeding during patrols (mean = 9.6%; SD = 15%; range: 0–44%; $n = 23$ patrols) compared with 35% of their time feeding during matched control periods (SD = 25%; range: 0–82.5%; $n = 23$ controls).

Additional Complementary Analyses

Equal observation times

When I truncated the longer observations within pairs to match the observation times of their counterparts, results were largely similar to those obtained with unequal observation times. With equal observation times patrolling chimpanzees spent more time traveling (Wilcoxon signed-rank test, $T = 162.5$, $P < 0.0001$), less time feeding ($T = 56$, $P = 0.02$), and covered longer distances ($T = 210.5$, $P < 0.0001$) than during matched control periods. Actual travel rate, however, did not differ between patrols and controls when the length of the observation was equalized ($T = 4.5$, $P = 0.91$).

Matched male numbers

When I selected control observations by matching to the maximum or average number of males present during scans, results were again largely similar to those obtained in the original analyses. Patrolling chimpanzees spent more time traveling than they did during control samples both when the maximum number of males was similar ($T = 161.5$, $P < 0.0001$) and when the average number of males was similar ($T = 162.5$, $P < 0.0001$). They also spent less time feeding than during controls (maximum number of males: $T = 101.5$, $P < 0.0002$; average number of males: $T = 82.5$, $P < 0.0002$) and covered longer distances (maximum number of males: $T = 213.5$, $P < 0.0001$; average number of males: $T = 216.5$, $P < 0.0001$). Actual travel rate, however, did not differ between patrols and controls when male numbers were closely matched (maximum number of males: $T = 44.5$, $P = 0.24$; average number of males: $T = 12.5$, $P = 0.74$).

DISCUSSION

The results of the preceding analyses reveal that territorial boundary patrols have tangible effects on the travel and feeding of chimpanzees. During patrols, chimpanzees at Ngogo spent more than half of their time traveling, on an average, but less than

10% of their time feeding. The opposite pattern emerged during normal activities; with chimpanzees spending about twice as much time feeding (33%) as traveling (16%) during control sessions. Consistent with these time budget differences, chimpanzees traveled three times as far during patrols than control periods, although they did not travel more quickly while patrolling. Traveling longer distances involved appreciably greater energy expenditure.

Although chimpanzees clearly spent less time feeding when on patrol than during other times, the difference in feeding time is probably even greater than reported here. Data collection was biased against finding the hypothesized result; feeding records for controls included only the focal individual, but records during patrols included feeding by all visible individuals. The bias introduced by using ad lib data particularly affected the results when an infanticide led to cannibalism by one or few patrollers, while other chimpanzees ate nothing. In addition, the minimum feeding time recorded was 1 min; shorter bouts were rounded up to this length. Thus if an individual ate only one fruit, I counted it as 1 min of feeding time. This was far more likely to occur during patrols, when one or two patrollers might have grabbed a fruit or two as they passed under and investigated a food tree in their neighbor's territory.

Chimpanzees covered long distances while patrolling, but unlike male spider monkeys moving along territory borders [Shimooka, 2005], they did not travel faster than at other times. In fact, a comparison of full patrols to 2 hr focal samples suggested that patrolling chimpanzees traveled relatively slowly. This difference did not appear in additional complementary analyses. The cautious manner in which chimpanzees moved during patrols probably accounted for the fact that they did not travel quickly. Just as they interspersed short resting bouts between longer periods of travel to listen for chimpanzees in other communities, they also moved slowly while patrolling, watching and listening for signs of neighbors to direct their travel. During normal travel within their own territory, chimpanzees traveled directly from one spot to another between food trees and social groups. Their travel depended more on the locations of known destinations than attentiveness to their surroundings.

The cost of travel is positively related to speed [Taylor et al., 1982], but slow travel during patrols may not compensate for energy deficits that result from reduced caloric intake and increased caloric output. Chimpanzees pay transport costs while both foraging and patrolling, but net activity costs appear to differ. Normal foraging presumably leads to net energy gains, or at least energy balance, because chimpanzees take in energy while traveling relatively little compared with patrols. Patrolling

chimpanzees ate almost nothing while spending a lot of time covering considerable distances. The energy savings from slow travel probably do not compensate for these net activity costs.

I matched patrols to control samples that contained a similar number of males rather than selecting control samples with a similar overall party composition. Patrol parties tended to contain a higher proportion of males than parties at other times, and it remains possible that differences in travel and feeding between patrols and control samples are the result of party composition rather than patrolling per se. Large, primarily male parties are rare outside of the patrolling context, however, so the energetic costs documented in this study are real costs associated with patrolling regardless of whether they were an effect of patrolling behavior or travel in male-biased parties.

The results presented here support the hypothesis that male chimpanzees incur energetic costs during territorial boundary patrols and suggest that ecological factors may constrain the ability of male chimpanzees to patrol. Previously at Ngogo, Mitani and Watts [2005] found that while both fruit availability and party size predict the tendency to patrol, party size accounts for most of the variation. Although fruit availability scores tended to be higher on patrol days than on days that the chimpanzees did not patrol, patrols occurred even when there was a paucity of fruit [Mitani & Watts, 2005]. Ecological conditions may generally be favorable enough at Ngogo to reduce the energetic impact of fruit scarcity [Potts, 2008]. This accords with the suggestion that frequent territorial behavior at Tai may result from high food availability [Herbinger et al., 2001]. Feeding efficiency should be high when fruit is abundant; this would permit more time to invest in territorial activities, because individuals can readily replenish energy spent.

Frequent patrols also suggest that chimpanzees at Ngogo enjoy a positive energy balance. Individuals there were observed to patrol 30 times during the 280 days that I followed chimpanzees for more than 6 hr in 2003–2006. Thus they patrolled, on average, every 9.3 days (weekly patrol rate of 0.75). This rate is similar to that found by Watts and Mitani [2001] in 1998–1999, when Ngogo chimpanzees patrolled every 9.7 days (weekly patrol rate of 0.72). Patrols at Ngogo occur approximately twice as often as those at Gombe [~every 22 day, 1977–1982, Goodall, 1986] and Tai [≤every 14 days, 1984–1991, Boesch & Boesch-Achermann, 2000].

Mitani and Watts [2005] pointed out that due to the unusually large number of males at Ngogo, the per capita patrol rate does not differ between sites. However, overlap in patrol participation is high. For the 25 adult males who were alive throughout my study period, each participated in about half of all patrols (mean = 52%, SD = 10%, range = 37–70%).

Such high patrol participation suggests that many individual males at Ngogo do, in fact, participate in more patrols than males at other sites. For individual male chimpanzees, frequent participation in patrols exacts energetic costs that must be sustained by available food resources.

Territorial boundary patrols, like other behaviors, are considered adaptive if fitness benefits outweigh fitness costs. Researchers interested in the fitness value of a behavior frequently focus on identifying its potential benefits. In the case of territorial boundary patrolling in chimpanzees, several nonmutually exclusive benefits have been hypothesized to play a role in maintaining patrolling behavior. However, costs are another important part of the fitness equation. Sufficiently low costs may favor patrolling even when the fitness benefits are weak [Wilson & Wrangham, 2003]. The costs of boundary patrolling are generally assumed to be low [Manson & Wrangham, 1991; Wilson & Wrangham, 2003; Wrangham, 1999]. Patrolling chimpanzees seem to reduce the most severe risk, that of serious injury or death, by patrolling in large parties [Boesch & Boesch-Achermann, 2000; Goodall, 1986; Goodall et al., 1979; Mitani & Watts, 2005; Watts & Mitani, 2001; Wilson et al., 2001, 2002]. Patrols in my sample contained a minimum of nine males (mean = 16, SD = 6, range = 9–29, $n = 29$ patrols).

Patrols also exact energetic and opportunity costs [e.g. Herbinger et al., 2001; Mitani & Watts, 2005; Watts & Mitani, 2001; Wilson & Wrangham, 2003], but these, too, have been thought to be sufficiently low that even with weak potential benefits, territorial boundary patrolling behavior remains adaptive [Wilson & Wrangham, 2003]. Until now, however, no attempt has been made to quantify the energetic costs of patrolling behavior. As this study demonstrates, energetic costs may not be negligible. Patrolling chimpanzees incur nontrivial energetic costs, spending significantly more of their time budgets traveling and moving over significantly longer distances, while feeding much less than they do normally. As similar quantitative data from other chimpanzee research projects become available, it will be possible to assess the extent to which variability across study sites reflects underlying ecological differences that influence the energetic costs of patrolling. This study represents a first step toward resolving this issue and adds to our understanding of a prominent and striking behavior displayed by our closest living relatives.

ACKNOWLEDGMENTS

I thank the Uganda Wildlife Authority, Uganda National Council for Science and Technology, and the Makerere University Biological Field Station for permission to conduct research in the Kibale National Park. My research was approved by the

University Committee on Use and Care of Animals (UCUCA), University of Michigan. I am grateful to John Mitani, David Watts, Hogan Sherrow, William Wallauer, Ndagizi Lawrence, Mbabazi Godfrey, and Tumusiime Alfred for contributing data on patrols. I thank Kathy Welch at the University of Michigan Center for Statistical Consultation and Research for statistical assistance. J. Lwanga, L. Ndagizi, A. Tumusiime, G. Mbabazi, and A. Magoba provided assistance in the field. This project would not have been possible without the support and guidance of John Mitani. I am grateful to John Mitani, David Watts, Jacinta Beehner, Thore Bergman, Bobbi Low, Anthony Di Fiore (editor), and two anonymous reviewers for valuable discussion and comments on earlier versions of the manuscript. My research was supported by the National Science Foundation (BCS-0215622 and IOB-0516644 to John Mitani).

REFERENCES

- Aureli F, Schaffner CM, Verpooten J, Slater K, Ramos-Fernandez G. 2006. Raiding parties of male spider monkeys: insights into human warfare? *Am J Phys Anthropol* 131: 486–497.
- Boesch C, Boesch-Achermann H. 2000. *The chimpanzees of the Tai forest: behavioural ecology and evolution*. Oxford: Oxford University Press.
- Burt WH. 1943. Territoriality and home range concepts as applied to mammals. *J Mammal* 24:346–352.
- Campbell NA, Reece JB, Mitchell LG. 1999. *Biology*. Menlo Park, California: Benjamin Cummings.
- Caro TM, Collins DA. 1987. Male cheetah social organization and territoriality. *Ethology* 74:52–64.
- Cooper MA, Aureli F, Singh M. 2004. Between-group encounters among bonnet macaques (*Macaca radiata*). *Behav Ecol Sociobiol* 56:217–227.
- Cords M. 2007. Variable participation in the defence of communal feeding territories by blue monkeys in the Kakamega forest, Kenya. *Behaviour* 144:1537–1550.
- Crofoot MC. 2007. Mating and feeding competition in white-faced capuchins (*Cebus capucinus*): the importance of short- and long-term strategies. *Behaviour* 144:1473–1495.
- Gaston AJ. 1978. The evolution of group territorial behavior and cooperative breeding. *Am Nat* 112:1091–1100.
- Goodall J. 1986. *The chimpanzees of Gombe*. Cambridge, Massachusetts: The Belknap Press of Harvard University Press.
- Goodall J, Bandora A, Bergmann E, Busse C, Matama H, Mpongo E, Pierce A, Riss D. 1979. Intercommunity interactions in the chimpanzee population of the Gombe National Park. In: Hamburg D, McCown E, editors. *The great apes*. Menlo Park: Benjamin/Cummings. p 13–54.
- Grinnell J, Packer C, Pusey AE. 1995. Cooperation in male lions: kinship, reciprocity or mutualism? *Anim Behav* 49:95–105.
- Gros-Louis J, Perry S, Manson JH. 2003. Violent coalitionary attacks and intraspecific killing in wild white-faced capuchin monkeys (*Cebus capucinus*). *Primates* 44:341–346.
- Henschel JR, Skinner JD. 1991. Territorial behavior by a clan of spotted hyaenas *Crocuta crocuta*. *Ethology* 88:223–235.
- Herbinger I, Boesch C, Rothe H. 2001. Territory characteristics among three neighboring chimpanzee communities in the Tai national park, Cote d'Ivoire. *Int J Primatol* 22: 143–167.
- Hyman J, Hughes M, Searcy WA, Nowicki S. 2004. Individual variation in the strength of territory defense in male song

- sparrows: correlates of age, territory tenure, and neighbor aggressiveness. *Behaviour* 141:15–27.
- Kerbis Peterhans J, Wrangham R, Carter M, Hauser M. 1993. A contribution to tropical rainforest taphonomy: retrieval and documentation of chimpanzee remains from Kibale forest, Uganda. *J Hum Evol* 25:485–514.
- Kruuk H. 1972. The spotted hyena: a study of predation and social behavior. Chicago: Chicago University Press.
- Manson J, Wrangham R. 1991. Intergroup aggression in chimpanzees and humans. *Curr Anthropol* 32:369–390.
- Mech LD. 1994. Buffer zones of territories of gray wolves as regions of intraspecific strife. *J Mammal* 75:199–202.
- Mech LD, Boitani L. 2003. Wolf social ecology. In: Mech LD, Boitani L, editors. *Wolves: behavior, ecology, and conservation*. Chicago: University of Chicago Press. p 1–34.
- Mech LD, Adams LG, Meier TJ, Burch JW, Dale TW. 1998. *The wolves of Denali*. Minneapolis: University of Minnesota Press.
- Mitani JC. 2006. Demographic influences on the behavior of chimpanzees. *Primates* 47:6–13.
- Mitani JC, Amsler SJ. 2003. Social and spatial aspects of male subgrouping in a community of wild chimpanzees. *Behaviour* 140:869–884.
- Mitani JC, Watts DP. 2005. Correlates of territorial boundary patrol behaviour in wild chimpanzees. *Anim Behav* 70:1079–1086.
- Mitani JC, Merriwether DA, Zhang CB. 2000. Male affiliation, cooperation and kinship in wild chimpanzees. *Anim Behav* 59:885–893.
- Mitani JC, Watts DP, Muller MN. 2002a. Recent developments in the study of wild chimpanzee behavior. *Evol Anthropol* 11:9–25.
- Mitani JC, Watts DP, Pepper JW, Merriwether DA. 2002b. Demographic and social constraints on male chimpanzee behaviour. *Anim Behav* 64:727–737.
- Nishida T, Corp N, Hamai M, Hasegawa T, Hiraiwa-Hasegawa M, Hosaka K, Hunt KD, Itoh N, Kawanaka K, Matsumoto-Oda A, Mitani JC, Nakamura M, Norikoshi K, Sakamaki T, Turner L, Uehara S, Zamma K. 2003. Demography, female life history, and reproductive profiles among the chimpanzees of Mahale. *Am J Primatol* 59:99–121.
- Nishida T, Hiraiwa-Hasegawa M, Hasegawa KYT. 1985. Group extinction and female transfer in wild chimpanzees in the Mahale Mountains National Park, Tanzania. *Z Tierpsychol* 67:281–301.
- Noble GK. 1939. The role of dominance in the social life of birds. *Auk* 56:263–273.
- Packer C, Hilborn R, Mosser A, Kissui B, Borner M, Hopcraft G, Wilmshurst J, Mduma S, Sinclair ARE. 2005. Ecological change, group territoriality, and population dynamics in Serengeti lions. *Science* 307:390–393.
- Pepper JW, Mitani JC, Watts DP. 1999. General gregariousness and specific social preferences among wild chimpanzees. *Int J Primatol* 20:613–632.
- Pontzer H, Wrangham RW. 2004. Climbing and the daily energy cost of locomotion in wild chimpanzees: implications for hominoid locomotor evolution. *J Hum Evol* 46:317–335.
- Potts KB. 2008. Habitat heterogeneity on multiple spatial scales in Kibale National Park, Uganda: implications for chimpanzee population ecology and grouping patterns. PhD Thesis. Yale University, New Haven.
- Schaller GB. 1972. *The Serengeti lion*. Chicago: University of Chicago Press.
- Sergio F, Newton I. 2003. Occupancy as a measure of territory quality. *J Anim Ecol* 72:857–865.
- Shimooka Y. 2005. Sexual differences in ranging of *Ateles belzebuth* at La Macarena, Colombia. *Int J Primatol* 26:385–406.
- Smith RJ, Jungers WL. 1997. Body mass in comparative primatology. *J Hum Evol* 32:523–559.
- Sockol MD, Raichlen DA, Pontzer H. 2007. Chimpanzee locomotor energetics and the origin of human bipedalism. *Proc Natl Acad Sci USA* 104:12265–12269.
- Stamps JA, Krishnan VV. 1999. A learning-based model of territory establishment. *Q Rev Biol* 74:291–318.
- Struhsaker TT. 1967. Ecology of vervet monkeys (*Cercopithecus Aethiops*) in the Masai-Amboseli Game Reserve, Kenya. *Ecology* 48:891–904.
- Struhsaker TT. 1997. *Ecology of an African rainforest*. Gainesville: University Press of Florida.
- Sugiyama Y. 2004. Demographic parameters and life history of chimpanzees at Bossou, Guinea. *Am J Phys Anthropol* 124:154–165.
- Taylor CR, Heglund NC, Maloij GMO. 1982. Energetics and mechanics of terrestrial locomotion. 1. metabolic energy-consumption as a function of speed and body size in birds and mammals. *J Exp Biol* 97:1–21.
- Wakefield ML. 2008. Grouping patterns and competition among female *Pan troglodytes schweinfurthii* at Ngogo, Kibale National Park, Uganda. *Int J Primatol* 29:907–929.
- Wallace RB. 2008. Towing the party line: territoriality, risky boundaries and male group size in spider monkey fission-fusion societies. *Am J Primatol* 70:271–281.
- Wallis J. 1997. A survey of reproductive parameters in the free-ranging chimpanzees of Gombe National Park. *J Reprod Fertil* 109:297–307.
- Watts DP. 2000a. Grooming between male chimpanzees at Ngogo, Kibale National Park. I. partner number and diversity and grooming reciprocity. *Int J Primatol* 21:211–238.
- Watts DP. 2000b. Grooming between male chimpanzees at Ngogo, Kibale National Park. II. influence of male rank and possible competition for partners. *Int J Primatol* 21:211–238.
- Watts DP. 2002. Reciprocity and interchange in the social relationships of wild male chimpanzees. *Behaviour* 139:343–370.
- Watts DP. 2004. Intracommunity coalitionary killing of an adult male chimpanzee at Ngogo, Kibale National Park, Uganda. *Int J Primatol* 25:507–521.
- Watts DP, Mitani JC. 2000. Infanticide and cannibalism by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Primates* 41:357–365.
- Watts DP, Mitani JC. 2001. Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour* 138:299–327.
- Watts DP, Muller M, Amsler SJ, Mbabazi G, Mitani JC. 2006. Lethal intergroup aggression by chimpanzees in Kibale National Park, Uganda. *Am J Primatol* 68:161–180.
- Wilson ML, Wrangham RW. 2003. Intergroup relations in chimpanzees. *Annu Rev Anthropol* 32:363–392.
- Wilson ML, Hauser MD, Wrangham RW. 2001. Does participation in intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees? *Anim Behav* 61:1203–1216.
- Wilson ML, Britton NF, Franks NR. 2002. Chimpanzees and the mathematics of battle. *Proc Biol Sci* 269:1107–1112.
- Williams JM, Oehlert G, Pusey AE. 2004. Why do male chimpanzees defend a group range? *Anim Behav* 68:523–532.
- Wilson ML, Wallauer WR, Pusey AE. 2004. New cases of intergroup violence among chimpanzees in Gombe National Park, Tanzania. *Int J Primatol* 25:523–549.
- Wrangham RW. 1999. Evolution of coalitionary killing. *Yearb Phys Anthropol* 42:1–30.