Raiding Parties of Male Spider Monkeys: Insights into Human Warfare?

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ABSTRACT   Raids into neighboring territories may occur for different reasons, including the increase of foraging and mating opportunities directly or indirectly through the killing of neighboring rivals. Lethal raids have been mainly observed in humans and chimpanzees, with raiding males being reported to search purposefully for neighbors. Here we report on the first cases ever witnessed of raiding parties of male spider monkeys, a species expected to show such a behavioral tendency, given its similarity with humans and chimpanzees in critical socio-ecological characteristics, such as fission-fusion social dynamics and male-male bonding. Despite the high degree of arboreality of spider monkeys, all seven witnessed raids involved the males progressing single file on the ground in unusual silence. This is remarkably similar to the behavior of chimpanzees. The circumstances around the raids suggest that factors such as reduced mating opportunities, number of males relative to that in the neighboring community, and the strength of bonds among males could play a role in the timing of such actions. The raids did not appear to be aimed at finding food, whereas there is some indication that they may directly or indirectly increase reproductive opportunities. Although no killing was observed, we cannot exclude the possibility that spider monkey raids may be aimed at harming rivals if a vulnerable individual were encountered. The similarity of spider monkey raids with those of chimpanzees and humans supports the notion that lethal raiding is a convergent response to similar socio-ecological conditions. Am J Phys Anthropol 131: 486–497, 2006.   © 2006 Wiley-Liss, Inc.

Coalitionary killing of adult members of another group is an especially intense form of communal territorial activity, which occurs regularly in some social insects, but has been reported only in a few vertebrate species (reviewed in van der Dennen, 1995; Wrangham, 1999; Gros-Louis et al., 2003). Although rare, coalitionary intergroup killing has received much attention in recent years in the quest to understand the socio-ecological conditions for the evolutionary origin of human warfare (Goodall, 1986; Alexander, 1989; Knauft, 1991; Manson and Wrangham, 1991; Boehm, 1992; van der Dennen, 1995; Wrangham and Peterson, 1996; Otterbein, 1997; Wrangham, 1999; Boesch and Boesch-Achermann, 2000; Fergusson, 2001; Layton and Barton, 2001; Wilson and Wrangham, 2003). Coalitionary intergroup killing was reported in various contexts in different species of primates and carnivores, such as during intergroup encounters, attempted immigrations, and group takeovers (e.g., spotted hyenas: Boydston et al., 2001; wolves: Mech and Boitani, 2003; lions: Grinnell et al., 1995; African wild dogs: Creel and Creel, 2002; primates: Gros-Louis et al., 2003). Most attention, however, has been given to lethal raids of chimpanzees, not only because they are our closest living relatives, but also because such raids resemble simple forms of human warfare (Turney-High, 1971; Sillitoe, 1985; Goodall, 1986; Manson and Wrangham, 1991; Chagnon, 1992; van der Dennen, 1995; Keeley, 1996; Otterbein, 1997; Maschner and Reedy-Maschner, 1998; Gat, 1999; Wrangham, 1999; Boesch and Boesch-Achermann, 2000; Kelly, 2000).

Lethal raiding is an unusual form of aggression because it does not result from the escalation of an initial conflict (Wrangham, 1999). Lethal raids in humans and chimpanzees are characterized by the incursion of a coalition of males into the neighbors' territory and the surprise fatal attack against vulnerable neighbors (Gat, 1999; Wrangham, 1999; Kelly, 2000). Lethal raiding differs from other forms of coalitionary intergroup killing (see above) for two main reasons. First, it is an assault against neighbors rather than a defensive activity, such

as when strangers are encountered by territory residents during incursions in search of food or attempted immigrations. Second, the raiding individuals return to their own territory after the attack rather than becoming new group members, such as in group takeovers. As in humans, descriptions of chimpanzee lethal raids suggest the involvement of high coordination among raiding members and deliberate movement into the neighboring territory, apparently as a result of strategic planning (van Hooff, 1990; Boehm, 1992; Wrangham, 1999; Boesch and Boesch-Achermann, 2000).

Wolves are the only other vertebrates for which lethal raids have been reported, but the few detailed observations suggest that the main reason for incursions into neighbors' territory is to search for food, and the killing is an accidental consequence of meeting a few resident individuals (Peterson, 1977; Mech, 1994). These descriptions suggest that intruding wolves, like hyenas (Hofer and East, 1993), tend to avoid residents. By contrast, raiding chimpanzees appear to search for neighbors rather than food (Goodall et al., 1979; Wilson et al., 2004), and to intentionally move toward neighbors when they locate them, usually by hearing vocalizations (Boesch and Boesch-Achermann, 2000; Watts and Mitani, 2001; Watts et al., 2006), giving observers the impression that killing is the goal of chimpanzee raids (Goodall, 1986; Wilson et al., 2004).

There are other characteristics relevant to lethal raids that are shared by chimpanzees and territorial human populations (Ghiglieri, 1987; Rodseth et al., 1991; Boehm, 1992; Layton and Barton, 2001; van der Dennen, 1995; Wrangham, 1999; Mitani et al., 2002; Marlowe, 2005). They both live in social systems characterized by a high degree of fission-fusion dynamics, in which members of a large community are rarely all together because they split into subgroups of flexible membership. Such a social system not only sets the stage for subgroups of several males performing raids, but creates the possibility for those males to encounter vulnerable victims, either alone or in smaller subgroups (i.e., *imbalance of power*: Goodall, 1986; Alexander, 1989; Manson and Wrangham, 1991; Wrangham, 1999).

Another relevant shared characteristic is that males of the same community form strong bonds with one another and perform most territorial activities together. In male-philopatric chimpanzees, boundary patrols, incursions, and lethal raids are always done by males, although some females may join them (Nishida, 1979; Goodall, 1986; Wrangham, 1999; Boesch and Boesch-Achermann, 2000; Watts et al., 2006). Similarly, in territorial human populations, women rarely participate in warfare, and males are nearly always the perpetrators of lethal raids (Adams, 1983; Boehm, 1992; Maschner and Reedy-Maschner, 1998; Manson and Wrangham, 1991).

Several hypotheses have been put forward to explain the occurrence of lethal raids in chimpanzees, both in terms of the proximate mechanisms and the long-term functions (Wrangham, 1999; Wilson and Wrangham, 2003). They can be reduced to two main hypotheses. Lethal raids can be viewed as an extreme form of mate competition in which males kill rival males to defend access to their own females, and possibly to gain access to females from neighboring communities (Manson and Wrangham, 1991; Boesch and Boesch-Achermann, 2000). Another possibility is that lethal raids are an extreme form of intercommunity feeding competition in which males defend or expand their territory, thus increasing

the availability of food sources for themselves, the females of their community, and their offspring (Wrangham, 1999; Williams et al., 2004). Characteristics of the timing, consequences, and behavior during raids may help in discriminating between the hypotheses. For example, according to the mate competition hypothesis, a factor that could affect the timing of male raids is the low availability of mating opportunities in their own community. In addition, one of the consequences of raids could be that females visit or permanently transfer to the community of raiding males because the raiding males demonstrate the ability to conduct raids in the neighbors' territory in defiance of the resident males (cf. Manson and Wrangham, 1991; Ghiglieri, 1987; Boesch and Boesch-Achermann, 2000). Alternatively, according to the feeding competition hypothesis, raids are expected to occur when food sources are scarce, and the raiding party would spend a considerable amount of time feeding in the neighboring territory (Wrangham, 1999). However, certain patterns may support both hypotheses. For example, a male bias in lethal raiding victims may reduce the power of neighboring male coalitions, thus increasing the extent to which raiding males can protect both females and food resources in their own territory, while facilitating their access to both females and food resources in neighboring territories (Wrangham, 1999; Wilson and Wrangham, 2003).

As the debate is still open over the relative benefits achieved by male raids in terms of gaining access to other females, weakening rivals, or improving food sources (Wilson and Wrangham, 2003; Williams et al., 2004), data from other species would bring a useful comparative perspective. Furthermore, detailed descriptions of nonlethal raids might provide insights into underlying factors, as a short-term increase of mating or feeding opportunities can be achieved without the killing of rivals. So far, however, lethal or nonlethal raids resembling those of chimpanzees have not been described in other species.

We report on the first cases ever witnessed of raiding parties of male spider monkeys, one of the few other primate taxa that has been hypothesized to perform lethal raids (Manson and Wrangham, 1991; Wrangham, 1999). Like chimpanzees, spider monkeys are characterized by male philopatry, a high degree of fission-fusion dynamics, strong associations between males, and male cooperative territorial defense (Klein, 1974; Fedigan and Baxter, 1984; van Roosmalen and Klein, 1988; Symington, 1988, 1990; Chapman et al., 1995; Wallace, 2001). After describing the seven raids witnessed, we discuss our observations in light of the hypotheses put forward to explain raids in chimpanzees.

METHODS

Study site and subjects

The observations reported here were part of a long-term study of the behavior and ecology of two communities (Eastern and Western) of spider monkeys (*Ateles geoffroyi yucatanensis*) carried out in the forest surrounding Punta Laguna lake (20°38′ North, 87°38′ West, 14 m above sea level) within the Otoch Ma'ax Yetel Kooh Reserve in the Yucatan peninsula, Mexico (Ramos-Fernandez et al., 2003). The habitat consists of a mixture of old-growth, semi-evergreen medium forest (with trees up to 25 m in height) and 30–50-year-old successional forest (with trees up to 10 m in height). Although the monkeys

use the successional forest on a regular basis, they spend more time in the medium forest, and return to it to sleep.

Raids were observed during 2002–2003. The two communities have been intensively studied since 1997. The Eastern community, to which the raiding males belonged, was well-habituated to the human presence before our long-term study began. The Western community, on which the raids took place, was habituated during 1997. All monkeys were individually recognized.

At the beginning of our long-term study in 1997, the Eastern community consisted of 19 monkeys with only one sexually mature male and seven sexually mature females, whereas the Western community consisted of 34 monkeys with seven sexually mature males and 14 sexually mature females. At the beginning of 2002, the Eastern community consisted of 22 monkeys with six sexually mature males and five sexually mature females, all with unweaned infants. The number of sexually mature males was reduced to four in the course of 2002 because of the intracommunity coalitionary killing of the third youngest in April (Valero et al., in press), and the death of the fourth youngest in September. During 2002–2003, three sexually mature females immigrated into the Eastern community. During 2002–03, the Western community consisted of about 40 monkeys with 8–10 sexually mature males and 12–14 sexually mature females. The monthly proportion of reproductively cycling females in Figure 2 was estimated on the basis of 7.5-month pregnancy and 18-month lactation periods. These are the lowest figures reported in the review by Chapman and Chapman (1990), and thus are conservative estimates. In the case narratives, females with infants 18–24 months old were considered likely to be lactating.

Observational methods

The effort by our research team (i.e., time spent following and searching for monkeys of the two communities) was about 100 hr per month in 1997 and almost tripled in 1998 and 1999, to return to about 100 hr per month from 2000 until October 2002. Effort doubled from November 2002 when we started to have two systematic data-collection teams (each with at least two people) per day, one for each community. The monkeys were typically observed at a distance of 10–20 m, which allowed good-quality observations most of the time, given the forest structure and use of binoculars. Data were collected by well-trained field assistants, students, and established researchers. When monkey subgroups were encountered, a combination of data-collection methods (Altmann, 1974) was used: 20-min instantaneous sampling of individual activities and locations, focal animal continuous sampling of detailed individual behavior, and all-occurrence sampling of major events such as fission, fusion, aggression, and rare behaviors such as locomotion on the ground. When a raid was witnessed, a complete account of the entire event was recorded into a dictaphone, while the 20-min instantaneous samples of activities and locations and focal samples were continued when visibility permitted.

Ranging patterns were quantified using the instantaneous samples of locations collected since 1997. Ranging patterns of the two communities have fluctuated over the years, but have consistently remained in the southeastern and southwestern portions of the forest around the lake, with a relatively small overlapping area between them (Ramos-Fernandez and Ayala-Orozco, 2003;

Ramos-Fernandez et al., 2003; Fig. 1). Home ranges were estimated using the kernel method (Worton, 1989). During 2002–2003, the period when we witnessed the raids, the territory size of the raided Western community was about 1.1 km^2, with about 0.3 km^2 of old-growth forest.

RESULTS

We witnessed seven raiding parties both while following monkeys of the Eastern community (four cases) and while searching for monkeys in the territory of the Western community (three cases; Table 1). The first raid was observed on March 25, 2002, and the last on December 19, 2003. Each case was witnessed by 2–4 researchers and field assistants, who consulted one another to improve the accuracy of witnessed events. The first raid followed the longest period without reproductively cycling females (i.e., all females were either pregnant or lactating for 10 months) in the Eastern community since the start of our long-term study (Fig. 2). Although research effort varied during 2002–2003 (see Methods), the rates of witnessed raids were quite similar when corrected for effort: 0.25 per 100 hr for March–October 2002, and 0.18 for November 2002–December 2003. Interestingly, no case of raids was observed for 6 months between cases 6 and 7, while the research effort remained roughly the same. Here we describe in detail the seven well-observed cases (numbers corresponding to those in Table 1) and two other relevant observations.

Case 1

On March 25, 2002, at 6:05 AM, we encountered the four oldest sexually mature males of the Eastern community in an overlapping area of the ranges of the Eastern and Western communities. At 6:25 AM, they descended to the ground and started to walk slowly and quietly into the Western community's territory. They were very attentive, scanning and appearing to listen for sounds. At 6:44 AM, they encountered three females, probably from the Western community (we were unable to identify them because we could not get close to them, as they avoided the raiding males), one of which had an infant. About a minute later, the female with the infant started to alarm-bark. When the males climbed up a tree the female barked louder and then fled, followed by the males. After a brief pursuit the males slowed down, and continued to move slowly into the Western community's territory, following the three females. At 6:53 AM, one of the two females without an infant started barking. At 7:01 AM, the males seemed to follow the third female, but gave up rapidly. At 7:05 AM, the males ate a few fruits, and the three females left them. This was the first feeding bout since the males entered the neighboring territory. The males spent about 2% of their time feeding during the incursion. They fed a bit more on the way back to their territory. Three of the four males fissioned at 7:37 AM, and we followed the remaining male who reached his own territory at 8:15 AM.

Case 2

On the morning of October 11, 2002, we were following three sexually mature males of the Eastern community (there were only four in total after the death of two of the youngest sexually mature males in April and September 2002), including the oldest community male, when at about 7:45 AM they descended to the ground and
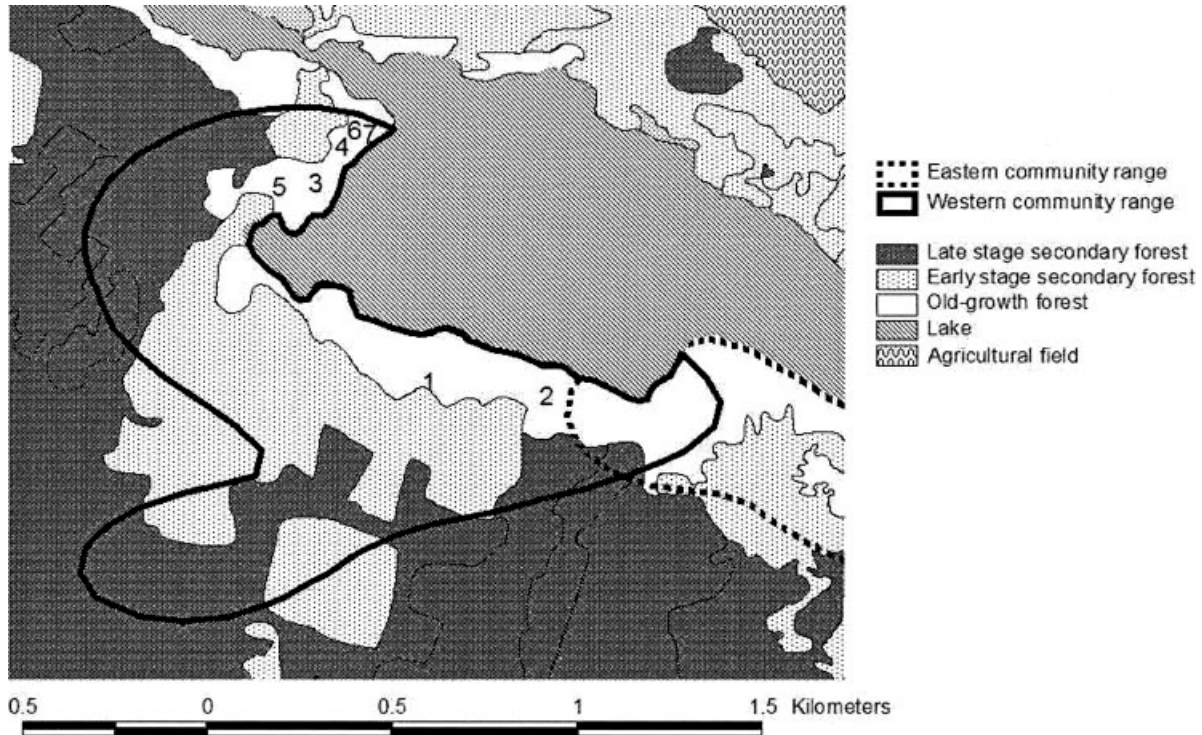
Fig. 1. Farthest location reached by Eastern community males during each raid into Western community territory. Numbers correspond to raid cases in Table 1.

started to walk silently in single file into the Western community's territory. Unfortunately, we lost them after a few minutes. We tried to find them by going to the same location where the Eastern community males went during their first witnessed raid. At 8:01 AM, we encountered a Western community subgroup. At 8:18 AM, while we were with this subgroup, we heard loud barking from a distance. We ran toward the location of the barking, where one of the females of the Western community subgroup had moved and may have been surprised by the raiding males. We did not find any females when we arrived at the location of the barking, but we did encounter the Eastern community males walking on the ground at 8:22 AM. We followed them. They moved quietly and attentively for a short time and then climbed up a tree, where they rested and groomed one another. They also ate briefly before moving and resting again, partially on the ground. At 9:28 AM, a female, known to have an infant and likely lactating, arrived at the same location of the raiding males. She was one of the females previously seen in the Western community subgroup, and was immediately attacked. The oldest and youngest of the raiding males grabbed her and bit her repeatedly (the third male participated little in the attack), while she vocalized loudly. She was rescued by her sexually mature son who suddenly appeared on the scene a few minutes later, running on the ground. When the oldest raiding male attacked the son, the mother defended him. The four monkeys (two raiding males and the two residents) fought for about 7 min, partially on the ground right in front of the four human observers, completely ignoring them. At 9:35 AM, the adult female and her son moved away from the scene. The Eastern community males did not follow them, and headed back into their territory. The infant, who was not seen during the whole

fight, joined the mother only when the raiding males were far away. Surprisingly, no monkey was seriously injured. The males returned to their territory at 10:15 AM, feeding for only 3% of the observation time during the whole raid.

Case 3

At 8:06 AM on March 1, 2003, all four sexually mature males of the Eastern community fissioned from a subgroup containing the majority of their community females and young, and started to travel on the ground toward the Western community territory, which they reached at about 8:20 AM. They continued to walk on the ground with only a few brief pauses, when they climbed about 1 m high into nearby trees. After one of these pauses at about 8:40 AM, one male left and went back to his home territory and rejoined the original subgroup. While walking on the ground, the males followed one another single file with their tails up and were extremely quiet, without producing any vocalizations or stepping on twigs that could make noise. They traveled fast, often stopping to scan the surrounding area by standing on two legs or climbing approximately 1 m into nearby small trees. Around 9:15 AM, an unidentified monkey, probably from the Western community, appeared to spot the raiding males walking, and dropped to the ground (it sounded like a large branch falling down) and tried to disappear into the undergrowth. The three raiding males chased the unidentified monkey for 20–30 m on the ground toward the lake from where we heard a brief scream and nothing more. Then, the three males went up into the nearby trees, looked around for a short time, and then went back where they were before the chase started. We investigated the area where the

TABLE 1. Details of seven witnessed cases of males raids

Case number	Date of raid	Start of raid[1]	End of raid[2]	Number of males involved in each raid	Duration of raid (in hours)[3]	Maximum distance[4] into neighboring territory (in meters)	Neighboring monkeys[5] encountered and behavior received from raiding males	Behavior of neighboring males[6]
1	25/03/02	Following monkeys	Males returned to own territory	4 (3 fissioned toward end)	1.8	550	3 unidentified females (1 lactating)	N/A
2	11/10/02	Following monkeys	Males returned to own territory	3	2.5	250	1 (likely) lactating female: severely attacked	1 male arrived and fought with raiding males
3	01/03/03	Following monkeys	Lost the males	4 (but 1 fissioned after 35 min)	2.7 (−)	1,450 (−)	1 unidentified monkey: chased	N/A
4	24/03/03	Searching for monkeys	Males (at least some) returned to own territory	4 (but 2 fissions of males)	3.0 (+)	1,600	1 lactating female 2 juvenile females 2 cycling females: chased, one for 10 min, and oldest raiding male disappeared with her	N/A
5	12/05/03	Searching for monkeys	Lost the males	4	0.4 (+,−)	1,350 (−)	Several unidentified monkeys, including females	2 males arrived, and raiding males disappeared
6	20/05/03	Following monkeys	Lost the males (but were already out of neighboring territory)	4 (but 1 fissioned after a few minutes)	3.0	1,900	1 lactating female 1 cycling female 1 unidentified female: severely chased	N/A
7	19/12/03	Searching for monkeys	Lost the males (but were already out of neighboring territory)	4	1.0 (+)	1,950	None	N/A

[1] Task that observers were involved in when they witnessed raid: Following monkeys, raid was witnessed from beginning; Searching for monkeys, raid had already started when males were encountered in Western community territory.
[2] How observation of raid ended: Males returned to own territory, end of raid was observed as males returned to own territory; Lost the males, the end of raid was not observed, as researchers lost males.
[3] Only time for which raid was observed; it could have been longer, as in some cases, raiding monkeys had been encountered while already in neighboring territory (marked with +), and in some cases, males were lost before they returned to own territory (marked with −).
[4] Distance could have been greater in some cases, as (some) raiding males were lost during incursion into neighboring territory (marked with −).
[5] Female, sexually mature female, unless stated otherwise. Reproductive state of sexually mature female is reported when known.
[6] N/A, not applicable because no neighboring males were encountered.
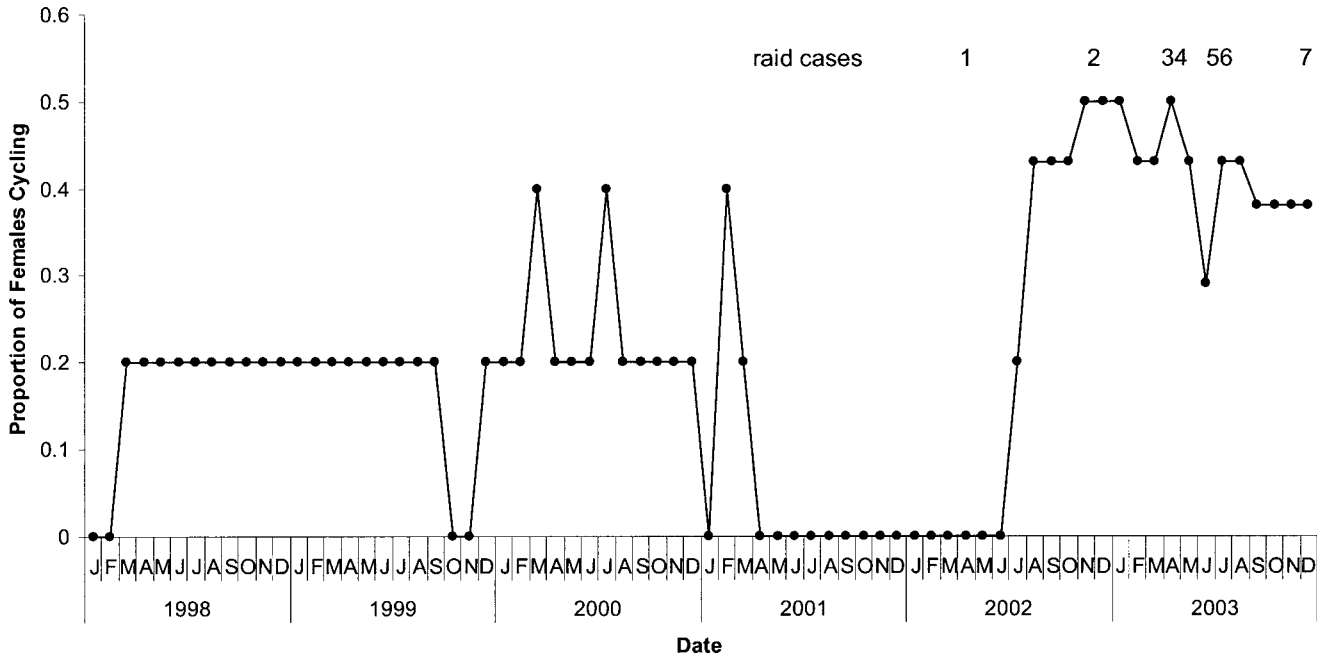
Fig. 2. Monthly (in each year, J–D corresponds to January through December) proportion of Eastern community females reproductively cycling (see Methods) during study period, and its temporal relation with seven cases of male raids (numbers correspond to raid cases in Table 1). Note that in first years, there was only one sexually mature male, whereas there were six when first raid occurred.

chase ended and where the scream came from, but we could not see the other monkey. Then, the males traveled on the ground silently and in single file, following the lake until 9:40 AM, when they finally stopped at about 1.4 km from their territory boundary. They briefly fed on fruits that were also widely available in their own territory. It was the first time they had eaten since they fissioned from their community subgroup. Then they rested for about 1 hr. At 10:50 AM, they started to head deeper into the neighboring territory away from the lake, moving from small tree to small tree. We lost them quickly due to the dense vegetation. The raid was one of the longest (about 3 hr before losing them). Remarkably, they spent most of the first 1.5 hr on the ground, virtually without feeding.

Case 4

At 1:35 PM on March 24, 2003, we encountered the four sexually mature males of the Eastern community while searching for monkeys in the Western community territory. The males walked quietly in single file on the ground for some time, always with the oldest male in the lead. At 2:10 PM, they encountered three adult females and two juvenile females of the Western community. Two of the adult females had an infant: one was very young, and the other was likely weaned (this was the same female that the raiding males attacked severely in case 2; by now, her infant was old enough to be weaned and thus she was likely reproductively cycling). The raiding males briefly chased the adult female without an infant, but then crept up on the adult female with the weaned infant, who was several meters away from the first adult female and seemed not to have noticed the males yet. The oldest two males immediately chased the adult female with the weaned infant, but

they appeared not to put effort in catching or harming her, as they waited for her to get away from them every time they went within arm's reach of her. The chase continued for about 10 min, until the oldest male chased the female off into the distance. Her infant was left behind with the other Western community females, who then also moved in the same direction as the chased female and the oldest raiding male. We stayed with the three remaining raiding males, who moved a little back toward their territory without going to the ground again. They spent time resting and socializing (especially the two oldest of these three males). At about 4:00 PM, they again moved slowly toward their territory with some feeding and resting until 4:30 PM, when the two oldest males chased the third male away and then returned to their own territory.

Case 5

While searching for monkeys quite deep in the Western community's territory, we encountered the four sexually mature males of the Eastern community at 8:20 AM on May 12, 2003. The males were on the ground, traveling silently in typical single file, with the oldest male in the lead. We followed them as they traveled along the lake, away from their own territory. At 8:45 AM, there was much confusion as the raiding males came across a subgroup of Western community monkeys. Several females scattered as soon as they saw the raiding males. Suddenly, a sexually mature male of the Western community came crashing through the forest, followed by another sexually mature male and a sexually mature female. The first male screamed and ran around as if he was looking for something (perhaps the raiding males). We did not see the raiding males after the arrival of the three Western community monkeys. From 9:00 AM, the

two sexually mature males from the Western community alarm-called and screamed for nearly 2 hr, constantly climbing trees and looking out across the lake.

Case 6

At 6:40 AM on May 20, 2003, we encountered the four sexually mature males of the Eastern community well within their own territory. They soon started to move rapidly from tree to tree in the direction of the Western community's territory. At 7:50 AM, they dropped to the ground and walked silently in single file, with the oldest male in the lead. One of the males fissioned shortly thereafter and returned to his own territory. At 8:15 AM, the raiding males encountered two sexually mature females of the Western community, one of whom had a young infant. The two females appeared very afraid, emitting distress vocalizations and scanning. The raiding males just sat on the ground, quite peacefully, until the females relaxed. After about 10 min, the two females left, and the males continued to travel on the ground in a different direction. We followed the males, but soon lost them. We found them again at 9:10 AM, when we heard screaming ahead, and an unidentified sexually mature female came crashing through the forest, pursued by the three raiding males. The males chased her to the edge of the lake, and then all four monkeys jumped into the lake. There was further screaming from the female and a lot of splashing by all the monkeys. It was difficult to determine whether the males were trying to attack the female or just trying to get out of the lake. After about 5 min, the males climbed back into the trees, but the female remained in the water. The three males wrapped their arms around each other (a typical behavior during coalitionary aggression), shook branches, and threatened the female, which appeared to prevent her from leaving the water. The female attempted to leave several times and then half-swam, half-waded across a little bay and vanished before the males could reach her by land. The males then rested for a short time by the lake, and traveled along the lake to return to their territory, having gone entirely around the lake. Unfortunately, at about 10:10 AM, we lost them due to poor visibility and difficult terrain, but by then they were out of the Western community's territory.

In cases 4–6, the raiding males spent virtually no time feeding while traveling into Western community territory, with less than 5% of the time spent feeding in total in the neighboring territory, mostly on their way back.

Case 7

At 12:57 PM on December 19, 2003, we encountered the four sexually mature males of the Eastern community deep inside the Western community's territory. They were walking silently single file on the ground, but when they saw us, they climbed into nearby trees. They continued their incursion, moving from tree to tree, and going farther into the neighboring territory along the lake. They did not descend to the ground again, and continued along the lake until they reached the outer boundary of the neighboring territory, which was not adjacent to their own territory (Fig. 1). After about 1 hr, we lost them when they went into an area of dense vegetation. During the witnessed part of the raid, the males mainly traveled and spent almost no time feeding.

TABLE 2. Characteristics of raids in chimpanzees and spider monkeys[1]

Characteristics of raids	Chimpanzees	Spider monkeys
Sexually mature males always involved	✔	✔
Females may join in	✔	
Walking on ground	✔	✔
Walking in single file	✔	✔
Silent, minimizing noise	✔	✔
Virtually no feeding	✔	✔
Pausing to scan and listen	✔	✔
Killing of neighbors	✔	

[1] ✔, characteristic is present in species.

An additional case

At 5:15 PM on February 25, 2003, we encountered three sexually mature males of the Eastern community in the Western community's territory. They were not on the ground, but it was dusk and they might have been settling down to sleep there, as it was late to be traveling back to their own territory. We did not consider this case with the others because we were with the males only a few minutes. However, it is interesting to report that the following day, a Western community female spent a few hours with the Eastern community males within their territory.

A further case by males from another community

On September 1, 2003, we observed three males belonging to an unknown community walking silently in single file on the ground in the Western community's territory. As soon as they saw us, the males ran away and disappeared. The three males (who could easily be recognized due to specific markings) had been seen with other unknown monkeys participating in an aggressive intercommunity encounter with members of the Western community 6 days earlier.

DISCUSSION

All seven raids involved 3–4 sexually mature males walking silently on the ground in single file for up to 1.5 hr, without spending much time feeding or resting. The males moved up to 2 km into the neighboring territory, entirely within the neighbors' highly used area of old-growth forest (Fig. 1). A whole raid may last for over 3 hr (Table 1; it could easily be longer than we witnessed, as sometimes we encountered raiding males already in the neighboring territory, or lost them due to the difficulty in following them on the ground).

Although multimale incursions into neighboring groups were reported in other monkey species (Sicotte and Macintosh, 2004), there are striking similarities between what we observed in spider monkeys and the behavior involved in boundary patrols and raids described in several chimpanzee populations (Table 2; Goodall, 1986; Nishida et al., 1999; Boesch and Boesch-Achermann, 2000; Watts and Mitani, 2001; Mitani et al., 2002; Wilson et al., 2004; Watts et al., 2006). The incursions were remarkably deep, given the 1.1-km^2 territory of the neighboring community (Fig. 1), which is toward the lower end of territory sizes reported for other spider monkey communities (1–4 km^2: Ramos-Fernandez and Ayala-Orozco, 2003), and much

smaller than chimpanzee territories (5–38 km^2: Nishida and Hiraiwa-Hasegawa, 1987; Herbinger et al., 2001; Watts and Mitani, 2001). Although the seven cases described in detail here involved the same 3–4 males, it is unlikely that raiding parties are a peculiar feature of the Eastern community males, as we observed three males belonging to an unknown community walking silently in single file on the ground in the Western community's territory.

Incursions into adjacent territories were reported from the four longest-term study sites with neighboring communities of chimpanzees (reviewed in Wrangham, 1999; Boesch and Boesch-Achermann, 2000; Mitani et al., 2002; Wilson and Wrangham, 2003), and lethal raids were witnessed or inferred in three of them: Gombe (Goodall et al., 1979; Wilson et al., 2004), Mahale (Nishida et al., 1985), and Kibale (Muller, 2002; Watts et al., 2006). At the fourth site, Taï in Ivory Coast, chimpanzees are usually in larger subgroups and are more rarely alone than at other sites (Boesch, 1996), suggesting that the conditions for an imbalance of power between aggressors and victims, which facilitates coalitionary killing, are less likely to occur (Wrangham, 1999; Boesch and Boesch-Achermann, 2000).

A similar argument was put forward to explain the absence of reports of lethal raids in bonobos (Wrangham, 1999), who share many characteristics with chimpanzees. This argument, however, may apply only to the study site of Wamba, where subgroups tend to be large (Kuroda, 1979; Kano, 1992); at Lomako, subgroup sizes are within the range found in chimpanzees (White, 1996; Hohmann and Fruth, 2002). Another explanation for the absence of lethal raids in bonobos is based on differences in intergroup interactions between the two *Pan* species, as bonobos appear to be less antagonistic (Idani, 1990; Kano, 1992; White, 1996). Alternatively, lethal raiding may not have been observed in bonobos because it is an event that arises from rare conditions. After all, it took 15 years, thousands of observations, and many intercommunity encounters before witnessing the first case in Gombe chimpanzees (Stanford, 1998). However, the fact that unlike chimpanzees, boundary patrols and incursions into neighboring territories have not been observed in bonobos (Kano, 1992; Hohmann and Fruth, 2002) makes it unlikely that coalitionary killing during raids will be observed.

No lethal raids have been reported in spider monkeys. One hypothesized reason for the lack of evidence in this genus could be that lethal raids do not occur because the highly arboreal lifestyle of spider monkeys (Campbell et al., 2005) reduces the effectiveness of coalitionary aggression (Wrangham, 1999). As for bonobos, an alternative explanation is that no sufficiently long-term study on fully habituated animals has been carried out on *Ateles* (Manson and Wrangham, 1991). This is especially true as raids are conducted on the ground, and high habituation to humans would certainly facilitate the observation of such risky behavior for a highly arboreal species. Furthermore, the research effort on spider monkeys is minuscule compared to that on chimpanzees. Thus, it is no surprise that raiding, although not lethal, was first witnessed in our Eastern community, likely the longest continuously studied and best-habituated community of spider monkeys.

Four of the seven witnessed raids resulted in coalitionary aggression against small subgroups of 1–3 neighboring monkeys. While in three cases, aggression was limited to (sometimes prolonged) chases, in case 2, a likely lactating female was severely attacked. Although no killing resulted from any of the raids, one may wonder what would have happened to the female victim in case 2 if her son had not rushed to her rescue. In case 5, at least two males and a female from the Western community arrived on the scene, crashing through the forest when some females scattered after spotting the raiding males on the ground. Their sudden and noisy arrival resulted in the disappearance of the raiding males. Such rescue actions were also reported in chimpanzees, in which individuals from the resident community came to the aid of vulnerable victims, scaring intruders away (Boesch and Boesch-Achermann, 2000; Muller, 2002; Watts et al., 2006).

As expected if lethal raids are aimed at reducing the power of neighboring male coalitions (see introduction), all but one of the 11 victims of lethal raids in chimpanzees were males (Wilson et al., 2004). This male bias may have some implications for interpreting our observations. Killing may not have occurred in the seven raids we witnessed because the Eastern community males never surprised a vulnerable resident male. Western community males were seen only in two raids (cases 2 and 5), when they came to rescue females who first encountered the raiding males.

The Eastern community males are certainly capable of coalitionary killing, as they killed a male from their own community a week after the first witnessed raid (Valero et al., in press). Thus, they may perform lethal raids under the appropriate circumstances, i.e., if they find an isolated and vulnerable male victim. However, these circumstances may be less common than for chimpanzees. Given that spider monkeys live in smaller territories (see above) and at higher densities (6–87 individuals/km^2: Ramos-Fernandez et al., 2003) than chimpanzees (1–5 individuals/km^2: Nishida and Hiraiwa-Hasegawa, 1987; Boesch and Boesch-Achermann, 2000), other residents could more easily hear victims' distress vocalizations and come promptly to their rescue. It is also possible that, as in bonobos, relationships between males of different communities are less antagonistic in spider monkeys than in chimpanzees. No interaction other than antagonism has been reported between chimpanzee males of different communities, apart from the initial phases when a community splits into two. In contrast, in the first part of our long-term project, we witnessed Western community males not only interacting aggressively, but also exchanging friendly behavior with Eastern community males during extended visits in Eastern community territory (Ramos-Fernandez, unpublished data).

Regardless of whether the outcome is lethal, spider monkeys may actually engage in raids, at lower rates than chimpanzees due to their high degree of arboreality (Campbell et al., 2005). It is therefore remarkable that Eastern community males spent prolonged periods on the ground in all but one case (case 7) in which they were observed in the Western community's territory. Being on the ground may be beneficial for a raiding party, because intruders may be less easily detected by members of other communities when moving quietly on the ground than when moving from tree to tree. This interpretation is supported by the few cases in which Eastern community males were seen on the ground in their own territory. In most cases, they briefly moved on the ground for a surprise attack against a member of their own community (for other cases of male use of the

ground to avoid being detected, see Campbell, 2003; see also Milton's case 25 in Byrne and Whiten, 1990, p. 23). Females and juveniles were never seen walking on the ground in the same manner.

Habituation to observers is unlikely to have played a role in the timing of the first witnessed raid, as the Eastern community monkeys were habituated before our long-term study began in 1997. In addition, the timing of the first raid cannot be attributed to a lower amount of effort by our research team before March 2002, as the effort was similar or even higher before that date (see Methods). Although we may have missed cases, the increased effort from November 2002 influenced the number of observed raids, as 5 of 7 cases were observed after this date. However, the rates of witnessed raids were quite similar when corrected for effort. Thus, research effort did seem to influence the witnessing of cases after the first raid, but there was no actual change in overall frequency of the monkeys' behavior.

A factor that could have affected the timing of the Eastern community raids is the number of sexually mature males relative to that of the neighboring community, a factor central to the imbalance of power hypothesis (Wrangham, 1999). There is observational and experimental evidence supporting the importance of this factor in chimpanzees. Parties with more males are more likely to patrol (Mitani and Watts, 2005) and to approach extra-community males (Boesch and Boesch-Achermann, 2000; Watts and Mitani, 2001), and experimental playback of loud calls of an extragroup male elicits stronger cooperative responses from larger parties of male chimpanzees (Wilson et al., 2001; Herbinger and Boesch, 2004). In the case of spider monkeys, the number of sexually mature males in the Eastern community increased from one at the beginning of our long-term study to six at the time of the first witnessed raid, whereas the number of males in the Western community did not change as much. This relative change would have therefore increased the relative power of the Eastern community males.

The larger number of males in the Eastern community is also likely to have increased mating competition within the community, which could have prompted raids in order to increase mating opportunities. Such competition could have been the cause of the intragroup male coalitionary attacks in the Eastern community observed during the month before the first witnessed raid. These attacks had a lethal outcome, as one of the six males was eventually killed by an intracommunity male coalition a week after the first raid (Valero et al., in press). Although the loss of one male reduced the relative power of the Eastern community, the intracommunity coalitionary attacks against a common enemy might have strengthened the bonds between the other males, thereby facilitating the initiation of raids by increasing coordination and trust for such risky behavior.

The timing of our first witnessed raid could support the mate competition hypothesis, as it followed the longest period without reproductively cycling females in the Eastern community since the start of our study. However, during the following 21 months in which we observed the other six raids, there was no clear relationship between their timing and the availability of cycling females in their own community (Fig. 2). Thus, although decreased mating opportunities within a community may prompt males to carry out raids in order to increase mating, it would appear that once raiding is triggered, it continues for several months.

When Eastern community males encountered Western community females during five raids (probably six, but in case 3, the encountered monkey could not be sexed), they behaved toward them in ways that are in accordance with increasing mating opportunities. As reported in chimpanzees (Goodall et al., 1979; Nishida and Hiraiwa-Hasegawa, 1985; Goodall, 1986; Boesch and Boesch-Achermann, 2000; Watts et al., 2006), the raiding males did not physically attack females without young or with old offspring who were or could soon become potential mating partners, whereas they severely attacked a likely lactating female (case 2). In some cases, the Eastern community males chased females without any serious attempt to catch them. The chases were similar to the aggressive behavior that male spider monkeys typically direct to females of their own community (Fedigan and Baxter, 1984; Campbell, 2003; Slater et al., 2005). During one raid (case 4), after a chase of about 10 min, the older Eastern community male quietly disappeared with a neighboring female. The possibility that females visit or permanently transfer to the community of raiding males is probably not the primary reason for chimpanzee raids (Williams et al., 2004), but one observation suggests that it may be more important in spider monkeys. In the additional case in Results, we reported that the day after the Eastern community males were seen in the neighboring territory at dusk, one Western community female spent a few hours with them within their territory.

Our observations do not bear much support for the feeding competition hypothesis, as the males spent virtually no time feeding during the incursions. The little feeding they did in the neighboring territory was mainly done after they encountered neighboring monkeys and on food sources also available in their own territory, suggesting that foraging was not the main reason for the raids (as in chimpanzees: Wilson et al., 2004). Spider monkey raids may have long-term effects in the expansion of their own territory and the increase of food sources by reducing the power of the neighboring male coalition, but at the moment, we do not have evidence for these effects. The observation of the severe attack on a lactating female (case 2) could, however, fit the feeding competition hypothesis if the female is viewed as a feeding competitor rather than a mating partner (cf. Williams et al., 2004).

Although comparisons of human warfare with coalitionary intergroup killing in other animals, especially chimpanzees, have raised objections (e.g., Power, 1991; Sussman, 1999; Kelly, 2000; Ferguson, 2001), we believe that our observations of spider monkey raids are useful for the debate on the origin of human warfare. Coalitionary intergroup killing in humans and chimpanzees could be interpreted as a result of homology derived from a common ancestor (e.g., Wrangham and Peterson, 1996, p. 47), but this interpretation is weakened by the apparent lack of such lethal attacks in the closely related bonobo (Marchant and McGrew, 1991; cf. Manson, 1991). The similarity of spider monkey raids with those of chimpanzees and humans advocates that the basis of coalitionary intergroup killing is a matter of a convergent response to similar socio-ecological conditions, such as fission-fusion social dynamics and male-male bonding (cf. Manson and Wramgham 1991). This interpretation strengthens the view of using the chimpanzee as a referential model for human evolution (Ghiglieri, 1987; Wilson and Wrangham, 2003).

Our observations, although in favor of the explanation of lethal raids as a convergent response rather than due to common ancestry, are not fully supportive of the current interpretation of their evolution. As there is no evidence for cooperative hunting in spider monkeys, the similarity of spider monkey raids with those of chimpanzees and humans could challenge the proposal of a link between group hunting and lethal raids based on the occurrence of both in humans and chimpanzees, but of neither in bonobos (Goodall et al., 1979; van Hooff, 1990; van der Dennen, 1995; Wrangham, 1999).

CONCLUSIONS

We cannot draw any firm conclusions from only seven raids. However, we noted some intriguing similarities with chimpanzees, suggested factors affecting the timing and possible functions of raids, and discussed their possible relevance to the understanding of human warfare. First, like chimpanzees, spider monkey males progress in single file on the ground, and are unusually silent during raids. The similarity, which is especially remarkable given that spider monkeys are otherwise almost entirely arboreal (Campbell et al., 2005), suggests that such characteristics are critical for the success of raids.

Second, the circumstances around the first witnessed raid suggest that several factors could play a role in the timing of such actions. One possible factor is that the reduced mating opportunity in their own community may make males take risks to search for other females. Another factor is that spider monkey raids also seem to depend on an imbalance of power (Manson and Wrangham, 1991; Wrangham, 1999), as indicated by the fact that Eastern community males started to raid after their number increased relative to the number in the Western community. A critical factor is possibly the strength of bonds among males to assure trust and coordination during the risky raids, but these are difficult to operationally define and thus measure.

Third, the behavior of raiding males and resident monkeys during encounters can give us some indication about the function of spider monkey raids. Like in chimpanzees, raiders appear to be searching for neighbors, not for food. Some of our observations are in agreement with the possibility that raids may directly or indirectly increase reproductive opportunities, but mating was not actually witnessed. Although no killing was observed, raiders might harm or kill male rivals who are sufficiently vulnerable. However, encountering such targets may be less likely than in chimpanzees, due to the higher probability that other residents come to their rescue. In addition, even given such low-cost opportunities, spider monkeys may have lower motivation for lethal attacks than chimpanzees, due to the possibly less antagonistic nature of the relationships between males of neighboring communities.

Finally, the similarity of spider monkey raids with those of chimpanzees and humans suggests that a broad comparative perspective may help in elucidating the factors and conditions underlying warfare. Such perspective should not only incorporate all cases of lethal raids, but would also benefit from the inclusion of well-detailed cases of nonlethal raids, as shown by our observations. In addition, it would be beneficial if the comparative perspective is broadened to integrate cases of intergroup coalitionary killing in species with strong male-male bonding, but with a low degree of fission-fusion social dynamics, such as capuchin monkeys (Gros-Louis et al., 2003).

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