The Cost of Defeat: Capuchin Groups Travel Further, Faster and Later After Losing Conflicts with Neighbors

Margaret C. Crofoot[1,2,3]*

[1]*Smithsonian Tropical Research Institute, Balboa, Ancón, Republic of Panamá*
[2]*Division of Migration and Immuno-ecology, Max Planck Institute for Ornithology, Radolfzell, Germany*
[3]*Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ*

ABSTRACT   Although competition between social groups is central to hypotheses about the evolution of human social organization, competitive interactions among group-mates are thought to play a more dominant role in shaping the behavior and ecology of other primate species. However, few studies have directly tested the impact of intergroup conflicts in non-human primates. What is the cost of defeat? To address this question, the movements of six neighboring white-faced capuchin (*Cebus capucinus*) social groups living on Barro Colorado Island, Panama were tracked simultaneously using an Automated Radio Telemetry System (ARTS), for a period of six months. Groups moved 13% (441 m) further on days they lost interactions compared with days they won interactions. To cover these larger distances, they traveled faster, stopped less frequently, and remained active later in the evening. Defeat also caused groups to alter their patterns of space use. Losing groups had straighter travel paths than winning groups, larger net displacements and were more likely to change their sleeping site. These results demonstrate that losing groups pay increased travel costs and suggest that they forage in low-quality areas. They provide some of the first direct evidence that intergroup conflicts have important energetic consequences for members of competitively unsuccessful primate social groups. A better understanding of how intergroup competition impacts patterns of individual fitness is thus needed to clarify the role that this group-level process plays in shaping the evolution of human- and non-human primate behavior. Am J Phys Anthropol 000:000–000, 2013.   © 2013 Wiley Periodicals, Inc.

Primate social systems (*sensu* Kappeler and van Schaik, 2002) are shaped, in part, by a fundamental tension between the selective pressures exerted by competition for resources within- vs. between-groups. On one hand, competition among group-mates over food limits group size (Wrangham et al., 1993; Krause and Ruxton, 2002) and, when resources are defensible, is hypothesized to promote nepotism and the formation of formal dominance relationships (Sterck et al., 1997). On the other hand, large, cooperative groups are predicted to have an advantage in conflicts with their neighbors, and thus, competition at the intergroup level may favor large group size (Wrangham, 1980) and egalitarian relationships (Sterck et al., 1997). Although competition between social groups is central to hypotheses about the evolution of human behavior and social organization (Boyd et al., 2003; Bowles, 2009; Puurtinen and Mappes, 2009), competitive interactions among group-mates are currently thought to play a more dominant role in shaping the behavior and ecology of other primate species (van Schaik, 1983; Janson, 1985; Terborgh and Janson, 1986; van Schaik, 1989; Sterck et al., 1997; Majolo et al., 2008; Schülke and Ostner, 2012). However, although the impacts of resource competition within primate groups are well documented (e.g., Janson, 1985; Koenig et al., 1998; Koenig, 2000; Vogel, 2005; Chancellor and Isbell, 2009; Foerster and Monfort, 2010; Kazahari and Agetsuma, 2010), the effects of competition between groups are not. Instead, indirect proxies like the negative relationship often found between group size and female

reproductive rate (van Schaik, 1983, Majolo et al., 2008; but see Robinson, 1988a, 1988b) serve as the primary evidence supporting van Schaik's (1983) contention that, in primates, the magnitude of the resources lost to competition with group-mates swamps the effects of competitive interactions with neighbors.

Does intergroup competition have important energetic implications for primates? Conflicts between neighboring social groups can impact resource access across a range of spatial and temporal scales (Crofoot, 2007), from the short-term exclusion of losers from specific resources (Janson, 1985; Harris, 2006) to the long-term annexation of highly productive parts of a habitat by competitively

successful groups (Harris, 2006; Pride et al., 2006; Mitani et al., 2010). Therefore, it is perhaps not surprising that the few studies to directly assess the costs (or benefits) of intergroup competition have yielded a range of often conflicting results (Janson, 1985 vs. Robinson, 1988a; Robinson, 1988b). These discrepancies relate, in part, to the scale of the analysis. Studies focused on the immediate impact of intergroup interactions report relatively small, transient effects (Janson, 1985; Markham et al., 2012), whereas those investigating the consequences of intergroup relationships have found evidence of sizeable differences in the resource access (Harris, 2006; Pride et al., 2006) and energetic status (Robinson, 1988a; Robinson, 1988b) of members of competitively successful vs. unsuccessful groups. One possible explanation for this apparent discrepancy lies in how the short-term costs of intergroup conflicts have been conceived and measured. Exclusion from a specific resource (e.g., a particular fruit tree—Janson, 1985) may not be the only, or even the principle cost of losing intergroup conflicts. Losing may also constrain a group's ranging options, preventing them from using their preferred foraging areas or routes and/or restricting their movement to low quality parts of their range.

To test this hypothesis, I compared the movement and space-use patterns of white faced capuchin monkey (*Cebus capucinus*) groups on days when they won vs. days when they lost agonistic intergroup interactions. If losing competitive encounters with their neighbors forces groups to forage in low quality parts of their range— areas where food density is low either because there are fewer or poorer quality food patches, or because resources have already been depleted—this change should have a measurable impact on their patterns of movement (Isbell et al., 1998). A decrease in resource density, for example, should increase the distance a group must travel each day to meet its metabolic needs (Isbell et al., 1998; Pontzer and Kamilar, 2009), assuming that group size remains constant (Asensio et al., 2009). To cover these larger distances, group members can either increase their travel speed (which has been shown to negatively impact the ability to detect new food resources—Janson and Di Bitetti, 1997), decrease the amount of time they spend in discretionary activities (like resting—Dunbar and Dunbar, 1988), or extend the length of their active period (i.e., continue to forage later into the evening—Lambert et al., 2009; Tan et al., 2013). Resource density should also impact the patterning of movement; groups are expected to stop and feed less frequently and the distance between subsequent stops is expected to be greater when resource density is low (Isbell et al., 1998). Foraging models also predict that under these conditions, individuals can improve their foraging efficiency by using less sinuous travel paths (i.e., moving in straight lines—Bartumeus et al., 2005; Turchin, 1998). Straight travel paths minimize the chance of revisiting previously exploited resources and, when resource density is low, increase the likelihood of discovering new food sources because they lead to high net displacement (de Knegt et al., 2007; Turchin, 1991). I thus predict that if conflicts with neighbors impact resource access, groups will have increased travel costs, ranging further and faster, stop less frequently, lengthen their period of activity, and will show less sinuous patterns of movement after losing such interactions. I hypothesize that this kind of decrease in resource access occurs because (1) groups retreat after losing conflicts,

causing them to backtrack and re-use parts of their range they have already exploited, or (2) losing disrupts groups' foraging strategies, forcing them to forfeit access to preferred (i.e. first choice) areas, and instead focus their foraging effort on other, presumably lower quality, parts of their range. If the first of these hypotheses is correct, groups are expected to recross their own travel paths more frequently (Kinnaird, 1992), enter fewer unique home range quadrats (Kinnaird, 1992), and be more likely to return to the previous night's sleeping site after losing an intergroup conflict. The second hypothesis, in contrast, predicts that losing groups will use straighter (i.e., less sinuous) travel paths that shift the focus of their foraging to a different part of their range, resulting in a greater daily net displacement.

METHODS

An Automated Radio Telemetry System (ARTS) was used to monitor the movements of white-faced capuchin monkeys, *Cebus capucinus*, living on Barro Colorado Island (BCI), Panama. Barro Colorado, the site of a Smithsonian Tropical Research Institute field station, is a 1500 ha island of semi-deciduous lowland forest that was isolated from the mainland in 1914 when the Chagres River was dammed to create Lake Gatun and the Panama Canal. It is home to a population of 250–300 capuchin monkeys in ~20 different social groups (Mitchell, 1989). In this population, home ranges overlap extensively and neighbors encountered one another relatively frequently (0.33 intergroup encounters per day— Crofoot, 2007). The outcome of intergroup interactions is influenced by the relative size of the competing groups, as well as by the location of the interaction (Crofoot et al., 2008).

Between 30 July and 6 August 2004, one or two capuchins from each of six neighboring social groups were captured and fit with radio-collars (see Crofoot et al., 2009). Groups ranged in size from 9–25 members (Crofoot, 2007). Individuals were chemically immobilized with Telazol (50 mg/ml of tiletamine hydrochloride, 50 mg/ml of zolazepam hydrochloride; Fort Dodge Animal Health, Fort Dodge, IA), a non-narcotic, nonbarbiturate injectable anesthetic, delivered via a Pneu-Dart CO_2 gun (Pneu-Dart, Williamsburg, PA). Outstretched hammocks were positioned below the sedated animals to catch them as they became drowsy and lost their grip (see Crofoot et al., 2009 for a full description of capture methods, including drug doses, physiological parameters, and recovery times). Once animals were on the ground and their heart rate, respiration, and temperature had been assured, each of them were fitted with a tubular nylon radio-collar (Advanced Telemetry Systems, Isanti, MN). The collars weighed 41 g, which was less than 2% of the body weight of the smallest individual we captured, and well within the recommended limit of 5% of a subject's body mass (Macdonald and Amlaner, 1980).

The capuchin groups were tracked using ARTS from November 2004 through April 2005. However, due to collar malfunctions, data for this entire period is only available for some groups (BLT, BL12, TB, and Top). The movement and space-use analyses presented here are restricted to these four groups, although data from all six groups were used to identify and characterize the outcome of intergroup interactions. In addition to the automated tracking, regular behavioral observations (six 3-hr follows per group, per month) were also conducted

from June 2004 through September 2005. All research received clearance from the Harvard University Institutional Animal Care and Use Committee (assurance no. A-3593-1) and complied with the laws of the Republic of Panama.

Automated radio telemetry

ARTS is a multiuser infrastructure that provides researchers with the ability to continuously and simultaneously monitor the location of a large number of radio-collared animals (for a detailed technical description, see Crofoot et al., 2008; Kays et al., 2011). It consists of seven 40 m radio towers, each topped with a fixed array of six directional antennas and connected to an automated receiving unit (for a detailed description of the receiving units, see Larkin et al., 1996). These receiving units are synchronized to scan through a list of radio frequencies corresponding to the transmitters worn by study animals. They record the relative strength of the radio signals across the fixed antenna arrays; these data are converted into bearings within a web-accessible PostgreSQL database, and the bearings are smoothed using signal processing software (PV-Wave, Visual Numerics, Inc., Houston, TX) to reduce noise. Locations are estimated from the smoothed bearings using an Andrew's M-estimator (Lenth, 1981a; Lenth, 1981b) implemented in the software program LOAS (Sallee, 2004). The accuracy of the ARTS system varies depending on location on BCI, but is ~50 m for the areas comprised in this study (Crofoot et al., 2008). Accuracy is not expected to vary depending on the outcome of intergroup interactions, and thus, comparisons of capuchin movements and space use on days when groups won vs. lost interactions should not be biased.

For this study, ARTS recorded the location of each study subject every 10 minutes for a period of 6 months, yielding a total of nearly 75,000 daytime location estimates for all study subjects combined. Data visualization and analysis were conducted in the software packages ArcGIS (ESRI, Menlo Park, CA, 94052) and Biotas (Ecological Software Solutions, LLC, Hegymagas, Hungary).

Data analysis

The further a primate group travels in a given day, the more likely they are to encounter one of their neighbors. This potentially confounding effect was controlled by only comparing days when intergroup interactions had occurred. To investigate the consequences of losing intergroup interactions, I compared the ranging behavior of adult females in four social groups on days when they won and lost interactions. I used two spatial criteria to identify intergroup interactions: (1) two groups approached to within 150 m of one another and (2) a clear displacement event occurred (one group remained at the site of the interaction for at least 20 min, while the other group left). The group that remained at the site of the encounter was considered to have won the interaction, whereas the group that left lost (Crofoot et al., 2008). These definitions were based on 23 intergroup interactions observed during behavioral sampling and are consistent with previous behavioral studies of intergroup interactions in primates (Kitchen et al., 2004; Harris, 2006).

The day ranges for each group were calculated by summing the distances between successive location estimates for each radio-collared study animal recorded by the ARTS system. ARTS did not yield location estimates for all sampling periods in a given day, and day range increased with the number of location estimates recorded. However, the relationship between day range and sample size reached an asymptote around 50–60 data points, and so only days with at least 60 data points (10 hours of data) were included in these analyses. I calculated the number of times a group stopped each day, as well as the total amount of time they were stationary. "Stopping" was defined as moving less than 10 meters in 10 minute period between relocations (Crofoot et al., 2010). Given the limited spatial resolution of the ARTS, this definition will yield both false negatives and false positives but it is not biased by whether a group won or lost an intergroup interaction on the day in questions, and thus, should allow us to compare the relative frequency of stops in these two conditions. Capuchins on BCI generally arrive at their sleeping tree and stop traveling sometime between 17:30 and 19:00 h (Crofoot, unpublished data). Therefore, I used the number of observation periods between 17:30-20:00 h in which groups were stationary as a proxy for how long the groups remained active each day. I determined the number of quadrats study groups used each day by overlaying a 50 m *50 m grid on the mapped day ranges in ArcGIS. I assessed the directedness of the capuchins' travel in two ways. First, I recorded the number of times per day each group recrossed its own travel path; second, I calculated each path's sinuosity, defined as the total path length divided by the net displacement (the distance between the path's start and ends points). Groups that ended their day within 100 m of where they began it (net displacement < 100 m) were considered to have returned to the same sleeping area.

To test the effect of winning vs. losing an intergroup interaction on capuchin movement (log transformed day range, travel velocity, active day length and sinuosity; stop number and stop duration) and space-use (net displacement, sleeping site fidelity, number of grid cells entered, and log transformed path re-crossing frequency), I fit generalized linear mixed models (GLMMs) using the *lme4* package in R 2.14.2 (R Development Core Team 2012). The major advantage of GLMMs is that they able to handle repeated measures and unbalanced sampling through the inclusion of random effects (Bolker et al. 2009). I included 'group identity' as a random effect in all models to account for repeated sampling of the same four study groups and to account for potential differences in group response. To control for potential seasonal differences in patterns of movement and rates of intergroup interaction, I separated the data into three 2-month 'seasons' based on differences in diet composition and food availability (Season 1: November-December; Season 2: January-February; Season 3: March-April). In Season 1, the availability of ripe fruit on BCI is low (Foster 1982) and capuchins increase the amount of time they spend foraging on insects (Mitchell 1989, Crofoot, unpublished data). In contrast, the capuchin diet is dominated by a single keystone fruit species, *Dipteryx oleifera*, in Season 2 (60-90% of feeding time– Crofoot, unpublished data), and in Season 3 consists of a wider range of fruit species and reduced reliance on insects (Crofoot, unpublished data). Including 'season' as a random effect did not significantly improve model fit, and so I dropped the term. I evaluated the significance of the fixed effect (outcome) using a likelihood ratio test of two nested models that differed only in the factor of
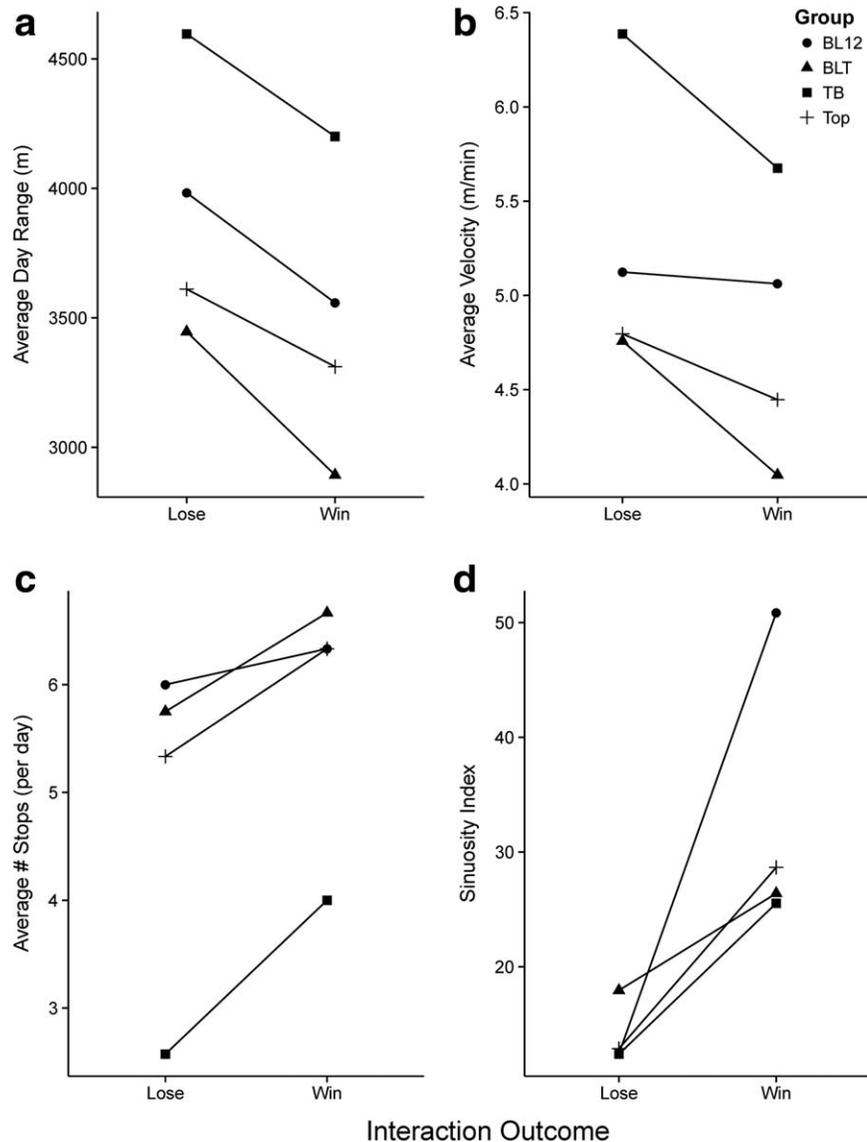
Fig. 1a–d: Impact of Intergroup Interaction Outcome on Group Movement Patterns. The average (a) day range (m), (b) velocity (m/min), (c) number of stops per day, and (d) sinuosity index (day range/net displacement) of the four white-faced capuchin groups in the study on days when they won vs. lost intergroup interactions. Generalized linear mixed models (GLMMs) treating 'group identity' as a random effect showed a significant relationship between intergroup interaction outcome and each of the movement variables at the α = 0.05 level (see Results).

interest. Significance for all tests was evaluated at α = 0.05.

RESULTS

Losing interactions increases travel costs

After controlling for the effect of group identity, capuchin groups moved 441 meters (13%) further on days they lost intergroup interactions than days they won interactions ($X^2 = 4.03$, df = 1, $P = 0.045$; Fig. 1a). As predicted if losing groups foraged in areas with lower resource density, they covered these larger distances by traveling faster, stopping less frequently, and remaining active for longer. Groups traveled 0.6 m/min (12%) faster on days when they lost interactions ($X^2 = 5.84$, df = 1, $P = 0.016$; Fig. 1b). They also made 17% fewer stops ($X^2 = 3.64$, df = 1, $P = 0.05$; Fig. 1c) and remained

stationary for 28% less time each day ($X^2 = 8.48$, df = 1, $P = 0.004$). The temporal distribution of "stops" suggests that groups also stayed active later on evenings when they had lost an intergroup interaction. They were stationary for 36% less time between 17:30 and 20:00 h on days when they lost interactions compared to days when they won interactions ($X^2 = 5.40$, df = 1, $P = 0.02$).

Losing groups alter their space-use patterns

The movement patterns of losing groups do not support the hypothesis that intergroup conflicts are costly because they force losers to retreat and to reuse recently exploited parts of their range. Groups in this study did not recross their own travel path more frequently on days when they lost intergroup interactions compared

with days when won ($X^2 = 0.74$, df = 1, $P = 0.39$) nor did they enter significantly fewer grid cells ($X^2 = 1.95$, df = 1, $P = 0.16$). Contrary to my prediction, the probability of re-using a sleeping site was significantly lower on days when groups lost interactions than on days when they won (3% vs. 24% probability of sleeping site re-use; $X^2 = 4.75$, df = 1, $P = 0.03$). Losing groups did, however, have straighter travel paths that resulted in greater daily net displacement. The travel paths of losing groups were significantly less sinuous (i.e., straighter) than those of winning groups ($X^2 = 4.01$, df = 1, $P = 0.045$, Fig. 1d), and the distance between where a group started and ended its day was nearly 80% larger when it had suffered a defeat ($X^2 = 7.24$, df = 1, $P = 0.007$).

DISCUSSION

The results of this study demonstrate that group-level competition in capuchin monkeys impacts the ranging behavior of losing groups, creating an energetic cost to subordinacy. Capuchin groups traveled nearly half a kilometer further on days when they lost conflicts with their neighbors, representing a 13% increase in day range. To put this effect in context, the difference in the day range length of winning vs. losing groups is roughly equal to the difference in the average day range of the smallest and largest groups in the study (BLT: group size = 9, day range = 3209 ± 726 m vs. BL12: group size = 25, day range = 3770 ± 684 m, see Fig. 1a).

In addition to the energetic costs associated with this extra travel, the longer, straighter day ranges, increased travel speeds, and decreased number and durations of stops indicate that losing groups were also ranging in areas with low resource density (Isbell et al., 1998; de Knegt et al., 2007; Pontzer and Kamilar, 2009). Losing capuchin groups stopped less frequently and for shorter periods, as would be expected if the fruit patches they were using were highly dispersed, small and quickly depleted (Isbell et al., 1998). However, due to the limited spatial resolution of the ARTS, it is not possible to differentiate between "stopping" to forage and "stopping" to rest. Thus, an alternate explanation is that after losing intergroup conflicts, capuchins reduce the amount of time they spent resting, perhaps in an effort to compensate for lost foraging opportunities (c.f. Janson, 1988). Their tendency to remain active later in the evenings after losing an intergroup interaction is consistent with this explanation.

Defeat disrupted capuchin space-use strategies. I found no evidence that losing caused groups to backtrack or re-use areas they had already exploited. Contrary to my prediction, in fact, groups were significantly less likely to re-use their sleeping site after losing an intergroup conflict. Whether this tendency to change sleeping sites exposes them additional costs, such as increased predation risk (Di Bitetti et al., 2000; Holmes et al., 2011), has yet to be explored. However, the patterns of space use documented in this study are consistent with the hypothesis that defeat forces groups to forfeit access to their preferred (i.e., first choice) foraging locations and move to other, presumably lower quality, parts of their range. Capuchin groups had straighter travel paths and larger net displacements after they lost interactions, as would be predicted if they were foraging in areas with low resource density. Future studies that measure habitat heterogeneity and resource

density will be needed, however, to directly test this hypothesis.

Is group-level competition costly? And, if so, what role does it play in shaping the evolution of non-human primate behavior? This study demonstrates the importance of considering a group's competitive success, rather than relying on size as a proxy for intergroup dominance, when addressing these questions. Although large size frequently confers an advantage in contests between primate social groups (Cheney, 1987; Cheney and Seyfarth, 1987; Robinson, 1988b; Kinnaird, 1992; Cowlishaw, 1995; Sugiura et al., 2000; Crofoot et al., 2008; Brown, 2011; Markham et al., 2012; Scarry, 2012), this advantage is by no means universal (Harris, 2010; Markham et al., 2012) or absolute (Robinson, 1988b; Sugiura et al., 2000; Perry, 1996; Crofoot et al., 2008). In fact, levels of cooperation among group-mates may play a larger role in determining the outcome of competitive intergroup encounters than the size of the competing groups (Crofoot and Gilby, 2012). As this study shows, the failure to compete successfully can lead to increased energy expenditure and decreased resource access for large and small groups, alike. Because competitive dynamics like these can influence the fitness of entire groups of individuals (Robinson, 1988b), they can have a major impact on patterns of population growth and demography (Packer et al., 2005; Courchamp et al., 2000). Whether such costs of "group subordinacy" are widespread, or are strong enough to act as selective pressures favoring the evolution of cooperative within-group behavior (via trait-group or multilevel selection, Wilson and Wilson, 2007) remains unclear (although see Willems et al., 2013 for a potential example). It is evident, however, that more needs to be known about how groups compete, grow, and multiply (Lehmann, 2011) if we are to understand the role intergroup conflict plays in promoting cooperative behavior in humans and other social species.

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