



Correlates of territorial boundary patrol behaviour in wild chimpanzees

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Territorial boundary patrols are a distinctive and unique aspect of wild chimpanzee, *Pan troglodytes*, behaviour. Although patrolling has been frequently observed in nature and several proposed functional explanations for it exist, scant information is available regarding the proximate factors that affect this activity. We found that there is considerable temporal variation in the frequency of patrolling by chimpanzees at Ngogo, Kibale National Park, Uganda. We examined several ecological and social factors that potentially influence this variation. Results of logistic regression analyses revealed that male party size was the single best predictor of the tendency to patrol. Lethal intergroup aggression occurs in chimpanzees, and patrols are likely to be dangerous and costly. Our findings are consistent with the hypothesis that chimpanzees at Ngogo reduce these costs by patrolling together in large parties.

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Long-term field studies continue to provide a rich set of observations to test hypotheses about the proximate causes and evolutionary function of animal behaviour (Altmann & Altmann 2003). Prolonged observation of individually identified animals in nature also furnishes the only means to document rare events that may have significant impacts on their lives. For example, the importance of infanticide in primates has long been debated, partly because observers do not witness it frequently. Extensive fieldwork, however, now clearly reveals that despite its rarity, infanticide is a pervasive threat in many primate species and has major effects on behaviour and reproduction (Watts 1989; Palombit et al. 1997; Borries et al. 1999; van Schaik 2000).

Wild chimpanzees, *Pan troglodytes*, have been the subjects of several long-term field studies (Goodall 1986; Nishida 1990; Boesch & Boesch-Achermann 2000; Wrangham 2000; Sugiyama 2004). These studies have enriched our understanding of several aspects of chimpanzee behaviour, including rare and unusual events such as hunting and tool making (Mitani & Watts 2001; Lonsdorf et al. 2004). Field observations show that chimpanzees reside in communities that contain multiple adult males, adult

females and immature individuals. Community members associate in temporary parties that vary in size, composition and duration. Encounters between individuals of neighbouring communities are typically hostile. Males defend territories by responding aggressively to intruders and by patrolling the boundaries of their own territories and entering those of their neighbours.

Territorial boundary patrols are one feature of chimpanzee behaviour that requires long-term field investigation for documentation and analysis (Goodall et al. 1979; Goodall 1986; Manson & Wrangham 1991; Wrangham 1999; Boesch & Boesch-Achermann 2000; Watts & Mitani 2001; Wilson & Wrangham 2003). Patrols are relatively rare events, occurring once every 10–23 days (Goodall 1986; Boesch & Boesch-Achermann 2000; Watts & Mitani 2001). During patrols, chimpanzees move to the periphery of their territory, where they search for signs of members of other communities. Chimpanzees may make deep incursions into their neighbours' territories while on patrol. Patrols include 8–13 individuals on average and are primarily a male activity, with the extent of female participation varying across sites (Goodall 1986; Boesch & Boesch-Achermann 2000; Watts & Mitani 2001). Patrolling chimpanzees are surreptitious; unless they encounter neighbours, patrollers remain quiet and refrain from performing conspicuous acoustic and olfactory displays like those characteristic of the territorial behaviour of other mammals (e.g. Robinson 1979; Mitani 1988; East & Hofer 1991; Sillero-Zubiri & Macdonald 1998; Harrington & Asa

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2003). Even when they hear neighbours, patrolling chimpanzees may silently retreat towards the centre of their own territory. In other cases, they respond to vocal or visual contact with neighbours by calling loudly and giving charging displays before retreating. In some encounters, patrollers launch coalitionary attacks on individuals of neighbouring communities. Such attacks can be lethal (review in Wilson & Wrangham 2003).

Patrols play an integral role in chimpanzee territorial behaviour, and three nonmutually exclusive functions for them have been proposed (Manson & Wrangham 1991; Wrangham 1999; Boesch & Boesch-Achermann 2000; Watts & Mitani 2001; Wilson & Wrangham 2003; Williams et al. 2004; Wilson et al. 2004). By patrolling and defending their territory, male chimpanzees may (1) improve their safety and that of other community members, (2) recruit new females into their community, either directly through coercion or indirectly by expanding the area that they control, and (3) maintain or even increase access to food for themselves, their mates and their offspring. The 'safety' hypothesis is upheld by definition, because outside males threaten all community members, except females with sexual swellings, with lethal aggression (Wrangham 1999). Lethal attacks by patrolling chimpanzees on neighbouring males reduce the probability that others can inflict fatalities on the patrollers' own community. Support for the 'female recruitment' hypothesis is equivocal. Although examples of this exist from studies of chimpanzees at Gombe and Mahale (Goodall et al. 1979; Nishida et al. 1985; Goodall 1986), secondary transfer by chimpanzee females is rare (Wrangham 1999), and females may shift or contract their ranges rather than transfer in response to territorial aggression (Williams et al. 2002). Current evidence is consistent with the 'food defence' hypothesis. Long-term data from Gombe indicate that intercommunity aggression leads to territorial expansion, resulting in higher female reproduction and larger foraging parties (Williams et al. 2004).

Although our understanding of the ultimate causes of chimpanzee territoriality and patrolling continues to improve, scant attention has been paid to the proximate factors that affect the relative costs and benefits of patrolling behaviour and thus influence the probability that males patrol on any given day. Several social and ecological factors are likely to influence these costs and benefits. Patrolling is a dangerous activity. Interactions between members of different communities are typically hostile and can result in fatalities, so patrollers risk attack by or retaliation from members of other communities. Males could reduce these risks by patrolling in relatively large groups (Manson & Wrangham 1991; Wrangham 1999; Wilson et al. 2001; Wilson & Wrangham 2003). Aspects of female life histories may also affect the costs of patrolling. Female chimpanzees reproduce very slowly, giving birth only once every 5–6 years to successive offspring who survive to weaning (Wallis 1997; Boesch & Boesch-Achermann 2000; Nishida et al. 2003; Sugiyama 2004). Male chimpanzees consequently show a keen interest in accompanying oestrous females (Matsumoto-Oda 1999; Wrangham 2000; Hashimoto et al. 2001; Anderson et al. 2002; Mitani et al. 2002a) and may suffer

opportunity costs by patrolling whenever potentially fertile females are present in their communities. Finally, the availability of food may affect the costs of patrols. Chimpanzees are highly frugivorous and principally eat ripe fruit, a resource that shows unpredictable temporal variation in availability. When fruit is scarce, chimpanzees increase their search effort to maintain relatively high fruit intake (Wrangham et al. 1998). Patrolling is energetically expensive. Patrollers move long distances and spend up to 6 h of a 12–13-h day engaged in this behaviour ($\bar{X} \pm \text{SD} = 2.13 \pm 1.01$ h, $N = 72$; J. C. Mitani & D. P. Watts, unpublished data). These considerations suggest that chimpanzees patrol primarily or exclusively during permissible ecological conditions when fruit availability is high.

We propose that one other factor may influence the benefits of patrolling. Chimpanzees enter the territories of their neighbours regularly, either while foraging in areas of overlap or during patrols. To deter incursions by neighbours, chimpanzees might increase the frequency with which they themselves patrol. Assuming that patrolling leads to successful defence, we expect the benefits of patrolling to increase when intruder pressure is high and predict that patrolling frequency varies positively with the frequency of territorial intrusions by others (cf. Boydston et al. 2001). Finally, additional theory suggests a link between chimpanzee patrolling and hunting behaviour. Drawing on the work of others (Eibl-Eibesfeldt 1975; Goodall et al. 1979; van Hooff 1990; van der Dennen 1995), Wrangham (1999, personal communication) has hypothesized that the hunting behaviour of chimpanzees evolved from their propensity to raid neighbouring conspecifics and that hunting vertebrate prey furnishes male chimpanzees with practise for patrolling. These ideas provide a rationale to investigate the effect of hunting on patrolling.

Since 1995, we have studied the behaviour of the Ngogo community of chimpanzees in the Kibale National Park, Uganda (Mitani et al. 2002b). Part of our interest in the behaviour of the Ngogo chimpanzees lies in the community's unusual size. With 142 individuals, the Ngogo community is significantly larger than other well-studied chimpanzee communities ($\bar{X} \pm \text{SD} = 46 \pm 20$, $N = 8$ communities; Mitani, in press). In prior research (Watts & Mitani 2001), we have shown that male chimpanzees at Ngogo are the primary participants in patrols and that they patrol about twice as often as chimpanzees at Gombe and Tai. Males at all three sites, however, patrol with equal frequency on a per capita basis. Thus, the high rate of patrolling at Ngogo is a simple consequence of the large number of males there. Regardless of its causes, the high frequency of patrolling by the Ngogo chimpanzees creates an ideal opportunity to investigate this behaviour in greater detail. In this study, we found that the tendency of the Ngogo chimpanzees to patrol varies considerably over time. We then analysed the effects of the previously discussed ecological and social factors on the observed temporal variation in patrolling. Our results clarify the proximate factors that affect patrolling activity and shed light on the ultimate causes underlying chimpanzee territorial behaviour and intercommunity aggression.

METHODS

Study Site and Animals

Data presented here were collected during 24 months spread over 5 years between 1999 and 2003. Ngogo lies at an interface between lowland and montane rain forest and is covered primarily with moist, evergreen forest. Butynski (1990), Struhsaker (1997) and Lwanga et al. (2000) provide detailed descriptions of the Ngogo study area. The Ngogo community is exceptionally large and contained 140–150 individuals with 22–24 adult and 13–15 adolescent males during the study period. Three adult males and two adolescent males disappeared and presumably died during this time. In addition, three adolescent males attained adulthood, and another four juvenile males reached adolescence.

We have used our extensive behavioural observations of the Ngogo chimpanzees, including interactions with neighbours, to define territorial boundaries. Since 1995 we have followed the Ngogo chimpanzees over approximately 25 km² (S. Amsler, unpublished data). To the south, this area borders the territory of the habituated Kanyanchu chimpanzees, whom the Ngogo chimpanzees occasionally meet. We have witnessed numerous inter-community encounters between the Ngogo chimpanzees and members of other adjacent communities; these help to delimit territorial boundaries to the north, east and west (Watts & Mitani 2000, 2001; Watts et al. 2002).

Behavioural Observations

We include observations from those days on which we maintained contact with the Ngogo chimpanzees for at least 6 h. Most days (623/683 days = 91%) during the 24 months of study satisfied this requirement. During following episodes, we recorded information regarding patrolling behaviour, male party size, presence of oestrous females, conspecific intruder pressure and hunting activity. We used spatial and behavioural criteria to define patrols. We identified patrols whenever chimpanzees (1) moved to and then along the boundary of their territory (30/72 cases, 42%) or into the territories of their neighbours (42/72 cases, 58%) and (2) displayed an unusual suite of behaviours (cf. Goodall 1986; Boesch & Boesch-Achermann 2000). During patrols, chimpanzees move in single file, maintain close proximity to each other and are uncharacteristically silent. In contrast, chimpanzee parties of similar size are usually scattered and noisy while individuals feed or travel. Patrolling individuals are extremely wary. They make frequent stops to scan the environment and are attentive to motion in the trees and on the ground; patrollers also sniff the ground and vegetation and inspect signs of chimpanzees such as nests, food wadges, urine and faeces. Chimpanzees rarely feed during patrols. Instead, they alter their normal foraging movements, occasionally making deep incursions into the territories of their neighbours. At Ngogo, patrols occur frequently and are easily recognized. Large, noisy parties typically form at this site (Mitani et al. 2002a), and the

conspicuous change in the movements and behaviour of individuals during a patrol is dramatic.

Chimpanzees live in fission–fusion societies whose members form temporary parties that vary in size and composition (Nishida 1968). If male numbers mitigate the costs of patrols, then the decision to initiate a patrol should depend on the number of males present at any given point in time. To test this hypothesis, we used the maximum number of adult and adolescent male chimpanzees that we observed associating each day. These numbers included counts of individuals who were together at one time during the day and typically reflected the maximum number of individuals present before the start of a patrol. An alternate measure is the number of males that actually patrolled together. Analyses using either variable yield the same results, and here we present those based on the maximum number of males. We also recorded the daily presence of oestrous females. In the field, these females are easily identified by their large sexual swellings. The Ngogo chimpanzees frequently hunt vertebrate prey (Mitani & Watts 2001; Watts & Mitani 2002), and we noted these hunting attempts ad libitum during following episodes. We additionally recorded ad libitum the times the Ngogo chimpanzees made aural or visual contact with members of other communities. Because we hypothesized that the frequency of territorial intrusions by members of other communities affected patrolling behaviour by the Ngogo chimpanzees, we counted only those encounters that occurred while the Ngogo chimpanzees were not actively patrolling themselves.

Fruit Availability

To assay the availability of fruit, we collected information regarding the phenology, density and size of fruit trees composing the top 20 species in the diet of the Ngogo chimpanzees. We combined these data to compute the following composite index:

$$\sum_{i=1}^{20} p_i \times d_i \times s_i$$

where p_i is the percentage of the i th tree species possessing ripe fruit; d_i is the density of the i th tree species (trees/ha); and s_i is the mean size of the i th species (cm dbh; see below).

We noted the presence or absence of ripe fruit in 20 trees of each species every month. Phenological observations were made during the sixth and 10th days of calendar months. Individual trees selected for sampling were randomly scattered across the Ngogo chimpanzee territory. We used diameter at breast height (dbh) to estimate tree size. For 15 tree species, we measured dbh of the 20 trees included in our phenological samples plus an additional 10 randomly selected individuals to calculate average tree sizes. For five tree species, we could not locate a sufficient number of individuals, and in these cases, dbh samples ranged from 22 to 28 trees. We recorded the densities of each species in 263 5 × 50-m plots placed randomly across the territory.

Statistical Analyses

We tallied the number of times that we observed patrols each month and divided this by the number of days per month that we followed the Ngogo chimpanzees. We multiplied this figure by the number of days in each month to derive a corrected frequency of patrolling per month. We used a chi-square goodness-of-fit test to evaluate heterogeneity in the tendency to patrol over time, with expected frequencies set to the 24-month average.

We used logistic regression to investigate the factors that affect the tendency of chimpanzees to patrol. We recorded whether chimpanzees patrolled each day and used these one-zero scores as the dependent variable. We examined the effects of five independent variables: male party size, fruit availability, intruder pressure, hunting activity and the presence of oestrous females. We used days as the unit of analysis for all of the independent variables. The presence or absence of oestrous females each day was assayed in discrete form, and the remaining four variables were defined continuously. We used records of male party size on patrol days, and on other days the chimpanzees did not engage in this activity. We computed fruit availability indexes and assigned them to the eighth day each month, the midpoint of phenological observations. We then linearly interpolated between these scores to create indexes for each day of observation. For example, fruit indexes of 300 and 600 calculated for 8 June and 8 July, respectively, would result in increments of 10 units every day between these two dates. We counted the number of days that intervened between each day in our sample and the time that chimpanzees last encountered members of another group. We used the number of elapsed days to assess intruder pressure. We constructed a similar score to assay hunting activity, replacing intergroup encounters with hunting episodes.

We recorded 72 patrols for which data on all five independent variables were available. To construct a balanced and representative sample of other days, we used a random numbers generator to select an equal number of days that chimpanzees did not patrol. We computed means of the four continuous independent variables for the samples of patrol and nonpatrol days and compared them with a Mann-Whitney *U* test. We performed bivariate logistic regressions to evaluate the independent effects of each of the five independent variables on patrolling. We conducted an additional multiple logistic regression using two variables shown to have significant effects, to assess their influence on patrolling when analysed together.

Ecological variables show considerable heterogeneity across months at Ngogo (cf. [Struhsaker 1997](#)). For example, rainfall varied from a low of 4 mm per month to a high of 340 mm over the 24 months of study ($\bar{X} \pm \text{SD} = 97 \pm 98$). Fruit availability also fluctuated widely during the course of our observations, with monthly scores of 4–1627 ($\bar{X} \pm \text{SD} = 743 \pm 445$). Patrols did not occur uniformly during sample months; we followed chimpanzees on 10 patrols during each of 2 months, but did not record any patrols in three other months ($\bar{X} \pm \text{SD} = 3 \pm 3$; [Fig. 1](#)). To guard against the possibility

that sampling a disproportionate number of patrols in some months biased our results, we performed an additional set of analyses using only one randomly selected patrol each month. Because we did not record patrols in 3 months, this resulted in a subsample of 21 patrols. We compared this subsample of patrols to a randomly selected control sample of 21 other days during which the chimpanzees did not patrol.

RESULTS

[Figure 1](#) shows the number of times the Ngogo chimpanzees patrolled during each month of observation. Patrolling did not occur uniformly over time ($\chi^2_{23} = 41.02$, $P < 0.02$). During some months, the chimpanzees patrolled frequently; in other months they did not patrol at all.

We examined five ecological and social factors hypothesized to produce the observed temporal variation in patrolling frequency through their effects on the costs and benefits of patrolling. Larger parties of males formed on days that males patrolled ($\bar{X} \pm \text{SD} = 18.1 \pm 6.2$) compared with other times (11.0 ± 6.8 ; Mann-Whitney *U* test: $Z = 5.55$, $N_1 = N_2 = 72$, $P < 0.001$). Similarly, fruit availability scores were generally higher on patrol days (812 ± 419) than on nonpatrol days (642 ± 447 ; $Z = 2.54$, $N_1 = N_2 = 72$, $P = 0.01$). Patrolling events occurred shortly after hunts, taking place significantly fewer days following a hunt (4.9 ± 8.2 days) than nonpatrol days did (6.5 ± 8.1 days; $Z = 2.12$, $N_1 = N_2 = 72$, $P = 0.03$). In contrast, intruder pressure, assayed by the number of days between a patrolling event and intercommunity encounter, did not appear to affect patrolling activity (patrol days: 28.9 ± 35.2 days; nonpatrol days: 24.5 ± 33.9 days; $Z = 0.97$, $N_1 = N_2 = 72$, $P = 0.33$). Oestrous females were present on 33% of all days that patrols took place (24/72), or fewer times than on days that patrols did not occur (44% = 32/72).

Results of the bivariate logistic regression analyses revealed that two variables had significant effects on the tendency to patrol ([Table 1](#)). Male party size had a significant effect on patrolling (Wald statistic: $W_1 = 27.20$, $P < 0.001$). The addition of one adult male to a party increased the odds of patrolling by 17% ($= (e^b - 1) \times 100$). The logistic regression model's fit to the data was significant and explained nearly 30% of the pseudovariance ($\chi^2_1 = 35.81$, $P < 0.001$; Nagelkerke $R^2 = 0.29$; [Table 1](#)). The proportion of days misclassified by the model (27%) represented a significant 46% reduction in the number expected without the model ($t_p = 0.46$; binomial test: $d = 5.52$, $P < 0.001$). Fruit availability also affected patrolling activity ([Table 1](#)). Observed values of the fruit availability index ranged between 14 and 1617, and increasing this index by a single unit increased the odds of patrolling by 0.10%. Despite its significant effect, this model explained only 5% of the pseudovariance, and resulted in a relatively modest 15% improvement in classification success rate ($t_p = 0.15$; binomial test: $d = 1.91$, $P = 0.06$). None of the three remaining variables, the presence of oestrous females, hunting activity or intruder

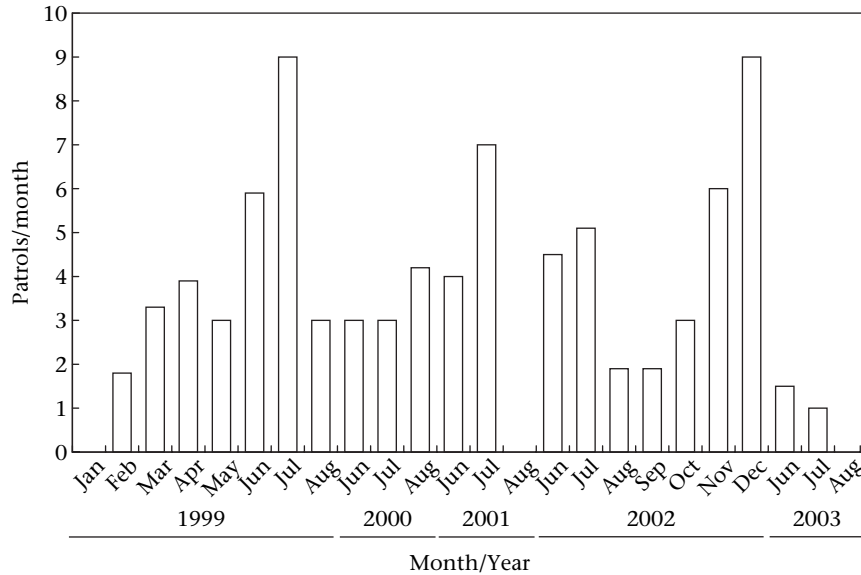


Figure 1. Temporal variation in territorial boundary patrol behaviour.

pressure, affected the chimpanzees' tendency to patrol (Table 1).

Previous analyses have demonstrated that male party size and fruit availability are correlated at Ngogo (Mitani & Watts 2005), a finding validated by the present data set ($F_{1, 143} = 6.75, P = 0.01$). Despite this relationship, collinearity between these variables was relatively low ($R^2 = 0.05$, tolerance = 0.95). To determine the best predictor of patrolling, we performed a multiple logistic regression analysis using male party size and fruit availability. When considered together, the two variables produced a model that fit the data and explained over 30% of the pseudovariance ($\chi^2_1 = 37.39, P < 0.001$; Nagelkerke $R^2 = 0.31$). Male party size was the only variable that displayed a significant influence on patrolling (Wald statistic: $W_1 = 24.83, P < 0.001$; Table 2).

Supplementary analyses conducted on the subsample of patrol days equally distributed across the 24 months of observation were consistent with those derived from the larger sample. Males formed larger parties on days when they patrolled ($\bar{X} \pm SD = 20.0 \pm 6.5$) compared with days when they did not patrol (10.2 ± 5.9 ; Mann-Whitney U test: $Z = 3.94, N_1 = N_2 = 21, P < 0.001$). Samples of patrol and nonpatrol days showed no differences in the three other continuous variables of fruit availability ($Z = 1.18, P = 0.24$), intruder pressure ($Z = 0.56, P = 0.57$) and hunting ($Z = 1.90, P = 0.06$). The presence

of oestrous females did not stop males from patrolling. Oestrous females were present on more days when males patrolled ($13/21 = 62\%$) than on days when patrols did not occur ($38\% = 8/21$). Finally, results of bivariate logistic regression analyses based on the subsamples of patrol and nonpatrol days confirmed the results using the entire sample; only male party size had a significant effect on the tendency to patrol (Table 3).

DISCUSSION

Results of these analyses indicate that the Ngogo chimpanzees show significant heterogeneity in their tendency to patrol over time. Much of this variation appears to depend on one factor, male party size. When the Ngogo chimpanzees gathered in parties with a large number of males, the odds of patrolling increased. In contrast, several other variables hypothesized to affect the proximate costs and benefits of patrols did not have a significant effect on this activity.

The presence of oestrous females and fruit availability influence chimpanzee party size (Chapman et al. 1995; Wrangham 2000; Anderson et al. 2002; Mitani et al. 2002a). Large parties of males typically form during times of high fruit availability and around oestrous females. Despite these relationships, the energetic costs of patrolling

Table 1. Bivariate logistic regression results showing the effects of five independent variables on patrolling events (analyses are based on patrols observed on 72 days during 24 months of observation)

Variable	<i>b</i>	SE	χ^2	<i>P</i>	R^2	e^b
Male party size	0.156	0.030	235.81	<0.001	0.29	1.169
Fruit availability	0.001	0.000	5.52	0.02	0.05	1.001
Hunting	-0.024	0.021	1.32	0.25	0.01	0.976
Oestrous females	0.470	0.345	1.86	0.17	0.02	1.600
Intruder pressure	0.004	0.005	0.62	0.43	0.01	1.004

Table 2. Multiple logistic regression results showing the effects of male party size and fruit availability considered together

Variable	<i>b</i>	SE	Wald statistic	<i>P</i>	<i>e^b</i>
Male party size	0.151	0.030	24.83	<0.001	1.162
Fruit availability	0.001	0.000	1.58	0.21	1.001

during periods of low fruit availability do not appear to deter male chimpanzees from doing so. Exceptionally good feeding conditions at Ngogo may contribute to the unusually large size of the community there, and this might lessen the energetic costs of patrolling even during bad times. Alternatively, males who are intent on patrolling might attract others to large parties during periods of low fruit availability, leading to the decoupling of any relation between patrolling and food availability. Further study is needed to explore these possibilities. Our results also suggest that the opportunity costs of losing chances to mate do not affect the occurrence of patrols. Determining the extent to which males lose reproductive opportunities while patrolling will require more precise information than is presently available regarding the exact times that females ovulate and data on paternity.

Lethal intergroup aggression is a characteristic feature of chimpanzee territorial behaviour (Wilson & Wrangham 2003). Why chimpanzees kill conspecifics is unclear. One prominent hypothesis suggests that dominance over neighbouring communities increases the availability of food resources and thereby improves female reproduction (Pusey 2001; Wilson & Wrangham 2003; Williams et al. 2004). Long-term observations at Gombe are consistent with this hypothesis by showing that temporal changes in territory size correlate positively with female reproductive success (Williams et al. 2004). Killing neighbouring conspecifics and territory expansion may also facilitate the recruitment of females and improve the safety of individuals (see Introduction).

Although chimpanzees may derive several kinds of benefits by killing their neighbours, to make an attack serious enough to result in a fatality is itself dangerous and costly. Our finding that male party size is the single best predictor of the tendency to patrol is consistent with the imbalance of power hypothesis, which attempts to explain why chimpanzees engage in lethal intergroup aggression (Manson & Wrangham 1991; Wrangham 1999; Wilson & Wrangham 2003). According to this hypothesis, the willingness of chimpanzees to make lethal attacks is principally affected by the costs of such aggression. These costs in

turn are sensitive to variation in male party size. Field observations indicate that male chimpanzees in large parties can launch attacks on others with little risk to themselves (Wilson & Wrangham 2003; D. P. Watts, J. C. Mitani, S. Amsler & H. Sherrow, unpublished data). Thus, the fission–fusion social structure of chimpanzees effectively produces low-cost opportunities for males to kill individuals of neighbouring groups. Over the short term, males can create such opportunities by forming large parties that have a good chance to outnumber those of any neighbours they encounter. The potential to produce these situations increases whenever the total number of males differs between communities. Over the long term, patrolling and lethal attacks can exacerbate such differences and make it more likely that power asymmetries occur during patrols and other encounters. Our results reveal that male chimpanzees at Ngogo attempt to reduce the costs of patrols and establish competitive asymmetries in their favour by making decisions to patrol when in large parties. Observations of the Tai chimpanzees conform to this picture by showing that patrolling frequency there declined over time as the number of males in the community decreased (Boesch & Boesch-Achermann 2000).

Several questions remain. Although our results suggest that the Ngogo chimpanzees modify their patrolling effort in response to its perceived risks, anecdotal observations indicate that other factors may influence this behaviour. Valuable food resources occasionally become available in abundance near territorial boundaries, and during these times, chimpanzees use these areas intensively. At Ngogo, chimpanzees appear to increase their patrolling frequency before such seasonal periods of food abundance, perhaps to assess the safety of the area. Whether patrols serve to ‘clear out’ such contested areas will require further study. Intergroup killing reduces the coalitionary strength of rivals and has been hypothesized to benefit patrollers by enhancing their feeding success and improving their safety (Wrangham 1999; Williams et al. 2004). Having gained these benefits, one might expect patrolling by chimpanzees to decrease following acts of lethal intergroup aggression. In the last 5 years, we have witnessed the Ngogo chimpanzees kill 12 members of different groups (Watts & Mitani 2000; Watts et al. 2002; Watts et al., unpublished data), but here too additional observations will be necessary to investigate this possibility.

Finally, territorial boundary patrol behaviour is unusual among gregarious mammals, having been documented only in chimpanzees and some social carnivores such as hyaenas and wolves (Sillero-Zubiri & Macdonald 1998; Boydston et al. 2001; Mech & Boitani 2003). The

Table 3. Bivariate logistic regression results showing the effects of five independent variables on patrolling events (analyses are based on a subsample of patrols observed on 21 days during 21 months of observation)

Variable	<i>b</i>	SE	χ^2	<i>P</i>	<i>R</i> ²	<i>e^b</i>
Male party size	0.231	0.068	19.32	<0.001	0.49	1.260
Fruit availability	0.001	0.001	1.66	0.20	0.05	1.001
Hunting	−0.066	0.045	2.66	0.10	0.08	0.936
Oestrous females	−0.971	0.635	2.40	0.12	0.07	0.379
Intruder pressure	0.005	0.011	0.26	0.61	0.01	1.005

ecological and social factors that affect the occurrence of patrolling in other mammals have not been explored in detail. Female spotted hyaenas, *Crocuta crocuta*, in the Maasai Mara, Kenya, patrol more than males do (Boydston et al. 2001). Female movements and their use of a clan's territory vary with reproductive state. Specifically, females spend less time near territory borders when they have young cubs (Boydston et al. 2003). Despite this variation in the use of space, lactating females participate in patrols and 'clan wars', as do pregnant and nonreproductive females (Boydston et al. 2001). Published studies do not indicate whether female reproductive state influences the rate at which individuals patrol or the probability that patrols occur on any given day. In addition, whether spotted hyaenas and other social carnivores seek to mitigate the costs of patrols, as chimpanzees do, by patrolling with many others remains an open question.

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