of increasingly economical new-generation high-throughput DNA-sequencing technologies can be expected to permit genome-wide definition of the primary phy-regulated transcriptional network through the use of ChIP-seq and RNA-seq procedures. Proteomic approaches, such as mass spectrometric analysis, may provide an avenue for unravelling the current enigma of the capacity of the phy molecule to induce phosphorylation of signaling partners *in vivo*, through direct interaction, in the absence of apparent evidence of autonomous protein kinase activity intrinsic to the photoreceptor molecule itself.

Where can I find out more?

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Lethal intergroup aggression leads to territorial expansion in wild chimpanzees

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Chimpanzees make lethal coalitionary attacks on members of other groups [1]. This behavior generates considerable attention because it resembles lethal intergroup raiding in humans [2]. Similarities are nevertheless difficult to evaluate because the function of lethal intergroup aggression by chimpanzees remains unclear. One prominent hypothesis suggests that chimpanzees attack neighbors to expand their territories and to gain access to more food [2]. Two cases apparently support this hypothesis, but neither furnishes definitive evidence. Chimpanzees in the Kasekela community at Gombe National Park took over the territory of the neighboring Kahama community after a series of lethal attacks [3]. Understanding these events is complicated because the Kahama community had recently formed by fissioning from the Kasekela group and members of both communities had been provisioned with food. In a second example from the Mahale Mountains, the M group chimpanzees acquired part of the territory of the adjacent K group after all of the adult males in the latter disappeared [4]. Although fatal attacks were suspected from observations of intergroup aggression, they were not witnessed, and as a consequence, this case also fails to furnish conclusive evidence. Here we present data collected over 10 years from an unusually large chimpanzee community at Ngogo, Kibale National Park, Uganda. During this time, we observed the Ngogo chimpanzees kill or fatally wound 18 individuals from other groups; we inferred three additional cases of lethal intergroup aggression based on circumstantial evidence (see Supplemental Information). Most victims were caught in the same region and likely belonged to the same neighboring group. A causal link between lethal intergroup aggression and territorial expansion can be made now that the Ngogo chimpanzees use the area once occupied by some of their victims.

From 1999 to 2008, the Ngogo chimpanzees utilized a territory of 28.76 km^2 (Figure 1A). During this period, they occasionally made forays into the territories of their neighbors on boundary patrols (Figure 1A). Patrols involve considerable travel, but little feeding or socializing; patrollers are unusually silent and move in single file line, while attending to signs of other chimpanzees [1]. Seventeen of the 18 observed fatal attacks were made by coalitions of Ngogo males on patrol (Supplemental Information). Thirteen of the 21 cases of lethal intergroup aggression (61.9%) occurred northeast of the Ngogo territory in a circumscribed region that corresponded to an area of heavy patrol activity (Figure 1B). Four victims were adult males, while 9 others were immatures. All 13 chimpanzees were unhabituated to human presence, and as a result, we do not know the exact size of their community. If its size is similar to those of chimpanzee communities studied elsewhere (X = 46.6, SD = 18.7, n = 8 communities [5]), the 13 fatalities represent a mortality rate of 2,790 per 100,000 individuals per year. Alternatively, a rate of 867 per 100,000 individuals per year results if one assumes the northeast community is as large as Ngogo's (150 individuals). These values are extremely high, exceeding median rates of mortality due to intergroup violence reported for humans in agricultural and hunter–gatherer populations by factors of 1.5–5 and 5–17, respectively [6]. They are also 23–75 times higher than the median rate suffered by individuals in nine well-studied chimpanzee communities [6].

Recent observations of the Ngogo chimpanzees reveal that they have expanded their territory considerably to the northeast into the area previously occupied by their neighbors (Figure 1B). Large, mixed-sex parties of Ngogo chimpanzees started to use this area regularly in June 2009, spending 43 of 132 observation days (32.6%) in the newly acquired territory over the next 5 months. They traveled, fed, and socialized in this region in ways

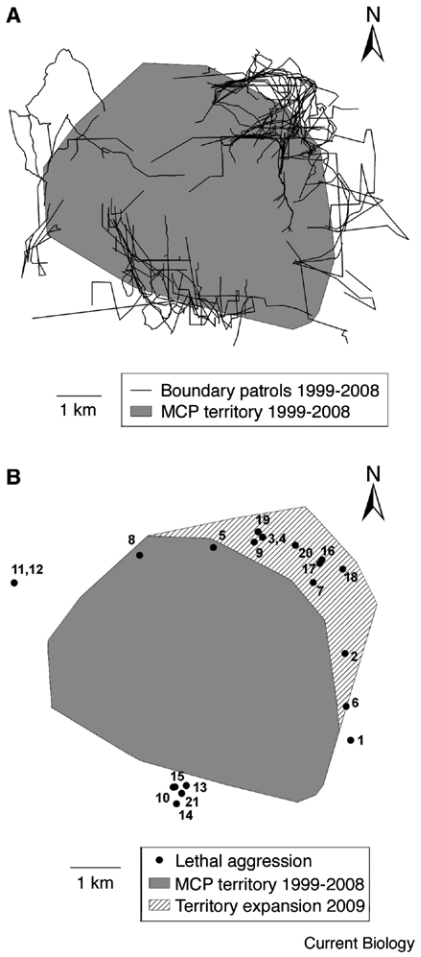

Figure 1. Territorial expansion and intergroup aggression in chimpanzees.

(A) The Ngogo chimpanzee community territory, 1999–2008. The 100% minimum convex polygon (MCP) territory shown in the shaded region excludes observations on days the chimpanzees conducted boundary patrols. Tracings of 114 territorial boundary patrols observed during 1999–2008 are also displayed. (B) Territorial expansion in 2009. The area excised from a neighboring chimpanzee community to the northeast is mapped in relation to the 1999–2008 MCP territory. Locations of lethal attacks made by the Ngogo chimpanzees on neighboring individuals are shown. Numbers correspond to cases listed in Table S1 in Supplemental Data.

similar to that in the central part of their territory. During this same time, neighboring chimpanzees were not observed in the area. This new area, equaling 6.4 km^2 and excised from their neighbor's former range, represents a 22.3% increase in territory size.

Our observations indicate that chimpanzees at Ngogo have expanded their territory at the expense of a neighboring community. Territorial expansion followed a series of lethal coalitionary attacks that formed an especially large source of mortality. The exceptionally large number of adult males in the Ngogo community likely contributes to their unusual success in intergroup conflict [5]. These findings are consistent with the hypothesis that lethal intergroup aggression reduces the coalitionary strength of opponents living in adjacent groups, leading to territorial expansion by the aggressors. Our observations help to resolve long-standing questions about the function of lethal intergroup aggression in chimpanzees. The suggestion that such aggression is an incidental by-product of human intervention is no longer viable [7]. Instead our findings support the hypothesis that killing neighboring conspecifics is adaptive. An unresolved question is whether chimpanzees do so to acquire mates or resources [1]. We cannot rule out the possibility that coalitionary attacks by Ngogo males may lead to new females joining their community [4], but results thus far are consistent with the resource acquisition hypothesis. By acquiring new territory through lethal coalitionary aggression, male chimpanzees improve the feeding success of individuals in their own community, which in turn can lead to increased female reproduction [8].

Human warfare is a heterogeneous phenomenon that varies with respect to who participates, what is involved, and why it occurs [9]. Because of this, whether chimpanzee intergroup aggression can be employed to provide insights into the origins and causes of warfare is likely to remain moot. Using our results to address an enduring question about why humans are an unusually cooperative species may prove to be a more productive line of inquiry. Our observations indicate that territorial conflict leads chimpanzees in some groups to cede land to members of other groups as a consequence of lethal coalitionary aggression. In the process, chimpanzees in communities that gain territory obtain increased access to resources that are then available to others in the group. Whether this selective factor can override the fitness costs suffered by individuals who cooperate within groups remains a theoretically and empirically challenging problem [10].

Supplemental Information

Supplemental Information is available at http://www.cell.com/current-biology/supplemental/S0960-9822(10)00459-8.

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