ANIMAL BEHAVIOUR

The evolutionary roots of lethal conflict

A comprehensive analysis of lethal coalitionary aggression in chimpanzees convincingly demonstrates that such aggression is an adaptive behaviour, not one that has emerged in response to human impacts. SEE LETTER P.414

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In 2013, there were 33 armed state-level conflicts around the world[1]. Many of these had persisted for decades, killed thousands of people and thwarted international peacekeeping efforts. War is certainly a contemporary fixture, but has it always been one? There is vigorous disagreement over the answer to this question. Some argue that warfare has been a pervasive feature throughout human history and has had important effects on human nature[2], whereas others contend that war is rare in foraging groups[3], the kinds of societies that we lived in for most of our evolutionary history. Debates about the origins and prevalence of human warfare are echoed in the question of whether lethal coalitionary aggression in chimpanzees has evolved through natural selection or whether it is a non-adaptive consequence of human disturbance. In this issue, Wilson *et al.*[4] (page 414) argue persuasively on the side of adaptation.

Many species of non-human primates have hostile relationships with members of neighbouring groups, and some species collectively defend the boundaries of their territories. But intergroup encounters rarely lead to serious injuries or deaths, perhaps because the risks of escalated aggression usually do not outweigh the benefits of killing opponents. Lethal coalitionary attacks on individuals from neighbouring communities have been documented only in chimpanzees. The first report of such killings was published 35 years ago[5], but the debate about their adaptive significance continues.

One point of view is that natural selection has favoured the evolution of lethal coalitionary intergroup aggression in chimpanzees as a means to enhance access to valuable resources, such as food and mates. Intergroup aggression might be more deadly in chimpanzees than in most other species because chimpanzees can exploit the imbalances of power that arise from 'fission–fusion' social organization[6]. Chimpanzees often fragment into temporary parties that travel and forage independently within their community's home range. When parties of males encounter single individuals from other communities, they sometimes launch brutal assaults that leave victims gravely wounded or dead (Fig. 1).

The opposing view is that lethal aggression is a non-adaptive response to anthropogenic influences, particularly artificial provisioning. In early primate field studies, researchers often used food to lure animals out of the forest, to facilitate close-range observation and to enhance habituation. At the Gombe National Park in Tanzania, where in 1962 primatologist Jane Goodall began providing bananas to chimpanzees who visited her camp, this practice had the desired effect. However, the chimpanzees began spending more and more time in the camp and rates of aggression among them increased. Provisioning was curtailed, and eventually terminated altogether. There were no reports of lethal aggression at Gombe before provisioning began, leading some researchers to conclude that these killings were the consequence of human intervention[7]. Subsequent reports of killings at other sites, where chimpanzees had never been provisioned, have been attributed to other forms of human intervention, including habitat loss[8].

Wilson *et al.* have comprehensively tested these two hypotheses by analysing 426 combined years of research at 18 chimpanzee (*Pan troglodytes*) study sites, and 92 years of research at 4 bonobo (*Pan paniscus*) study sites. The authors assembled information on all instances of lethal aggression that have been observed directly by researchers, inferred from the nature of the victim's injuries or suspected on the basis of the circumstances of their deaths or disappearances. Coalitional killings were documented at 15 of the 18 chimpanzee study sites, but there was only one suspected killing among bonobos.

The authors then tested how the frequency of killings by chimpanzees was affected by several variables linked to human impact, including provisioning and habitat disturbance, and a second set of variables related to the intensity of resource competition, including the number of males and population density. The statistical model that best fits the data includes variables linked to the intensity of resource competition, rather than those linked to human impact. Specifically, the authors' modelling shows that killings occur at higher rates in communities that have more males and higher population densities.

These results should finally put an end to the idea that lethal aggression in chimpanzees is a non-adaptive by-product of anthropogenic influences — but they will probably not be enough to convince everyone. Perceptions of the behaviour of non-human primates, particularly chimpanzees, are often distorted by ideology and anthropomorphism, which produce a predisposition to believe that morally desirable features, such as empathy and altruism, have deep evolutionary roots, whereas undesirable features, such as group-level violence and sexual coercion, do not. This reflects a naive form of biological determinism. Selective pressures alter traits as organisms move into new environments and confront new

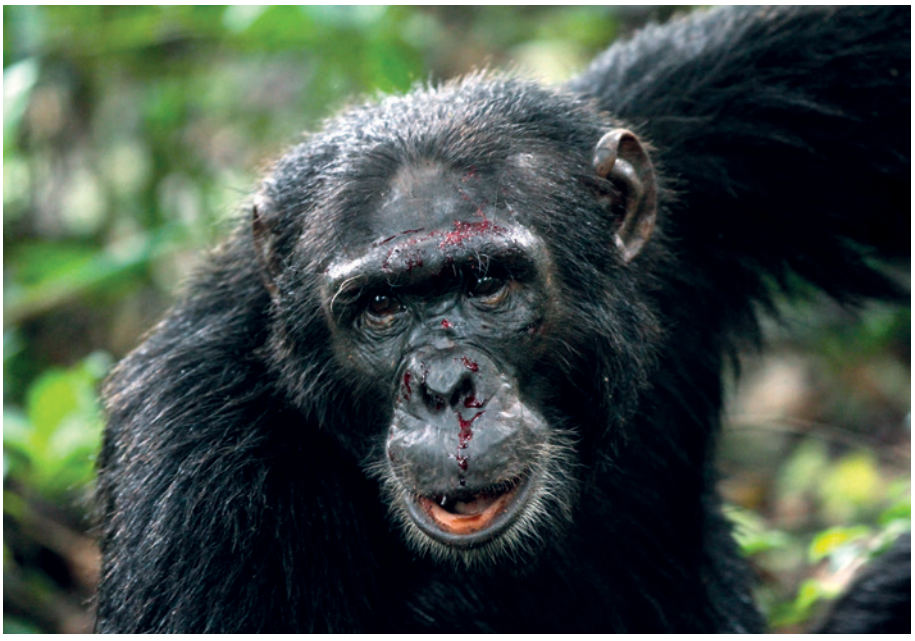

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Figure 1 | A male chimpanzee with fresh wounds following an inter-group attack.

challenges and opportunities. The data tell us that there are some ecological and demographic circumstances in which the benefits of lethal aggression exceed the costs for chimpanzees, nothing more. Humans are not destined to be warlike because chimpanzees sometimes kill their neighbours.

For those who are persuaded by Wilson and colleagues' evidence, a more interesting set of questions emerges. For example, how do chimpanzees overcome the collective-action problem? By eliminating rival males and infants sired by males from other communities, chimpanzees gain access to new territories and mating partners. But these benefits flow to the group as a whole, which creates opportunities for free-riding. Although the imbalance-of-power hypothesis relies on the odds being in the aggressors' favour, males forgo opportunities to mate and forage while they are on patrol, and run at least some risk of being injured in attacks. Do males that join patrols and lead attacks gain more benefits than those that remain in the security of their own community's territory? What forces curtail free-riding? The answers to these questions will provide interesting insight into the selective forces that favour group-level cooperation in species without language, social institutions and systems for sanctioning free-riders. ■

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ASTROPHYSICS

Giant black hole in a stripped galaxy

An oversized, supermassive black hole has been discovered at the centre of a densely packed conglomeration of stars. The finding suggests that the system is the stripped nucleus of a once-larger galaxy. SEE LETTER P.398

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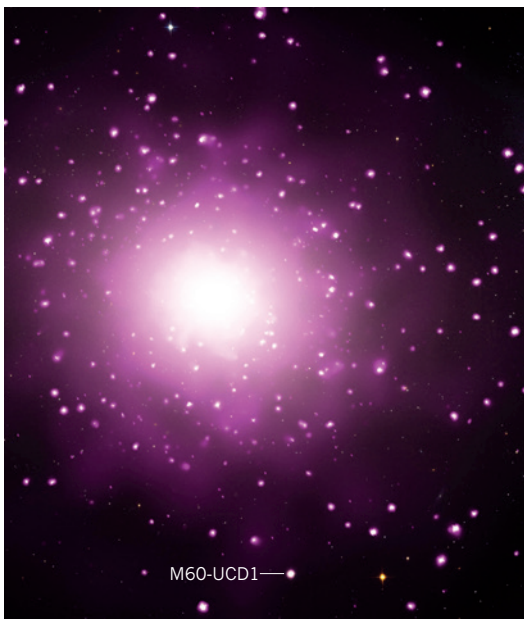
Supermassive black holes, which have masses millions or even billions of times that of our Sun, reside at the centre of almost every massive galaxy, including our Milky Way[1]. There seems to be some connection between the evolution of galaxies and that of these black holes, although the nature of the relationship is not well understood. What we do know is that, in general, bigger galaxies harbour bigger black holes at their centres, and these black holes are typically about 0.5% of the total mass of a spheroidal galaxy's stars[1]. But on page 398 of this issue, Seth *et al.*[2] report the detection of an oversized supermassive black hole that is a whopping 18% of the stellar mass of its unusual host.

The dense stellar system in which the black hole has been found, M60-UCD1 (ref. 3), is called an ultra-compact dwarf galaxy, and marks a previously unknown environment for supermassive black holes. Ultra-compact dwarf galaxies are densely packed spherical conglomerations of stars[4]. For years, astronomers have debated the nature of these objects — are they extremely massive star clusters, or are they the nuclei of galaxies that have had their outer layers stripped off through gravitational interactions with other galaxies? Seth and colleagues present the first clear case that an individual ultra-compact dwarf is a stripped-galaxy nucleus, because star clusters do not host supermassive black holes.



X-RAY: NASA/CXC/MSU/J. STRADER *ET AL.*; OPTICAL: NASA/STSCI

Figure 1 | Dwarfed by its neighbour. This composite image, constructed from data from NASA's Chandra X-ray Observatory and Hubble Space Telescope, depicts the massive elliptical galaxy M60 and the nearby ultra-compact dwarf galaxy M60-UCD1. Seth *et al.*[2] report that M60-UCD1 contains a supermassive black hole.

Seth *et al.* 'weighed' the black hole by determining its gravitational influence on nearby stars orbiting it[5,6]. To explain the observed stellar velocities and the distribution of light within M60-UCD1, they had to invoke the presence of a central black hole with a mass 21 million times that of our Sun. A black hole of that size would be expected to reside in a host galaxy with a mass of about 7 billion solar masses. However, Seth *et al.* estimate that M60-UCD1 has a stellar mass of only 120 million solar masses.

Although the discovery of an enormous black hole in such a small galaxy is surprising, recent work has uncovered a substantial number of black holes in other low-mass dwarf galaxies[7]. However, M60-UCD1 is clearly a different beast from those — it is far more compact and has a much more massive black hole. The small black holes in other low-mass dwarf galaxies are probably similar to the first 'seeds' of supermassive black holes[8]. Over cosmic time, such seeds grow by swallowing gas and coalescing with other black holes during galaxy mergers. With a mass 200 times that of the smallest nuclear black holes known, M60-UCD1's black hole seems to have already grown considerably.

So how did such a big black hole get into such a tiny galaxy? The answer may be related to M60-UCD1's galactic neighbourhood. This ultra-compact dwarf galaxy is right next door to the giant elliptical galaxy M60 (Fig. 1). Seth and co-workers' simulations show that M60-UCD1 may have formerly been a more massive galaxy than it is now (with a proportionally sized black hole), but lost most of its stars in a gravitational tug of war while orbiting its giant neighbour. What is left today is the dense stellar nucleus and central supermassive black hole from the larger progenitor galaxy.

The evidence for a supermassive black hole in M60-UCD1 is strong, but it is not the only possible explanation for the