

Intergroup Aggression in Wild Primates

Introduction

The papers presented in this Special Issue of *Behaviour* are the result of an invited symposium, *Intergroup Aggression in Wild Primates*, held at the XXIst Congress of the International Primatological Society in Entebbe, Uganda, June 25–30, 2006.

Intergroup aggression has long been a central topic in primate studies. Most primates live in groups, which may compete with other groups for access to resources such as territory, food, and mates. Intergroup aggression affects the spacing of social groups over the landscape, and in some species accounts for a high proportion of mortality. It has figured prominently in models of the evolution of primate social behavior, and is of interest to those seeking to understand the origins and evolution of human warfare.

Intergroup relations vary greatly among the primates. In some species, social groups may mingle peacefully, or simply avoid one another. In other species, groups exclude rivals from their territory, and in some species, including chimpanzees and humans, lethal raiding may occur. The reasons for this variation among species, and among populations of a given species, continue to be debated.

Efforts to develop and test socioecological models of intergroup aggression have yielded some points of consensus. Like aggression between individuals, aggression between groups is now widely considered to be a strategic option employed during competitive interactions, when assessment indicates that the net benefits will outweigh the costs. Benefits include access to mates, food, and protection of self, infants, and others. Males and females generally differ regarding which of these benefits limits their reproductive success, with males limited most strongly by access to mates, and females by access to food. Costs include time, energy, and the risk of injury or death, and may vary according to the number of opponents on each side, and their fighting ability and motivation. Variation among species results from an in-



This photo is from an intergroup killing between chimpanzees that took place in Kibale National Park in August 2006. The victim (on the ground) is already dead, having been killed about 15 minutes previously by a gang attack. The attacker (above the victim), delivering a kick to the victim's chest, is a young adult male member of the Ngogo community, who participated in the coalitionary attack (Photographer: John Mitani).

teraction among various factors, including the typical distribution of key resources.

This theoretical perspective has considerable heuristic value, but testing the relevant hypotheses has proven difficult for several reasons. In most species, intergroup encounters occur infrequently, and are often difficult to observe, due to rapid movements of multiple actors in areas of low visibility. Many studies have focused on a single habituated group. Few studies have quantified key measures, such as the abundance and distribution of food resources. Many hypotheses are not mutually exclusive, making it difficult to disentangle which factors are most important. Comparative studies have been hampered by the use of different methods for collecting and analyzing

data among sites. Finally, primates are a diverse group. The emergence of data from previously neglected species often presents challenges to older views and assumptions.

The papers in this volume represent recent efforts to overcome these challenges. The studies generally relied on longer datasets (median: 33 months), often used data from multiple study groups (median: 3 groups), and benefited from various methodological advances, including radio-telemetry and quantitative measurements of food resources. And while a limited number of papers cannot hope to do justice to the broad diversity of primates, this issue does provide a cross section of apes and monkeys from Africa, Asia and the New World.

Three major themes run through this issue. The first involves the question of the ultimate factors motivating intergroup aggression, in particular, food resources versus mates. Two papers (Crofoot; Robbins & Sawyer) test the relative importance of competition for food versus mates, while a third (Harris) provides a critical review of methods for distinguishing among these hypotheses. The second is variation among individuals. Despite the label "intergroup" aggression, the individuals within a group rarely respond in a uniform manner. Cords and Kitchen & Beehner focus on how and why individuals vary in their behavior during intergroup encounters. The third major theme is response to risk. Wich & Sterck examine how males respond to rival males posing different levels of threat, based on familiarity and life phase. The final two papers (Wrangham et al.; Wilson et al.) focus on risks posed by traveling in border zones.

Together these papers illustrate the current state of our understanding of intergroup aggression in primates, yet also indicate areas where future research is needed. In particular, the number of studies attempting quantitative tests of functional hypotheses remains small. Increased use of playback experiments will provide more controlled tests of key hypotheses.

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