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Chimpanzees and the mathematics of battle

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Recent experiments have demonstrated the importance of numerical assessment in animal contests. Nevertheless, few attempts have been made to model explicitly the relationship between the relative number of combatants on each side and the costs and benefits of entering a contest. One framework that may be especially suitable for making such explicit predictions is Lanchester's theory of combat, which has proved useful for understanding combat strategies in humans and several species of ants. We show, with data from a recent series of playback experiments, that a model derived from Lanchester's 'square law' predicts willingness to enter intergroup contests in wild chimpanzees (*Pan troglodytes*). Furthermore, the model predicts that, in contests with multiple individuals on each side, chimpanzees in this population should be willing to enter a contest only if they outnumber the opposing side by a factor of 1.5. We evaluate these results for intergroup encounters in chimpanzees and also discuss potential applications of Lanchester's square and linear laws for understanding combat strategies in other species.

Keywords: intergroup aggression; Lanchester battles; numerical assessment; chimpanzee; fighting; competition

1. INTRODUCTION

Observational studies support the expectation that larger groups should tend to win intergroup fights (Cheney 1987; Packer *et al.* 1990; Harcourt & de Waal 1992; Adams 1998; Gat 1999; Wrangham 1999). Recent experimental studies have demonstrated that, in several species, individuals are more willing to enter contests the more they outnumber their opponent (Adams 1990; McComb *et al.* 1994; Wilson *et al.* 2001). Nevertheless, few animal behaviour studies have attempted to model explicitly the relationship between numerical assessment and willingness to fight. Research on human warfare, however, includes a large body of literature devoted to such explicit models. In particular, models based on Lanchester's theory of combat (Lanchester 1916), widely used in operations research (Wallis 1968; Fricker 1998), should be applicable to intergroup contests in other species.

Lanchester proposed two models of attrition of opposing armies, the 'square law' and the 'linear law'. Both models assume that attrition depends on the number and fighting value of opponents on each side, with the relative importance of numbers compared with individual fighting value depending on the particular battle strategy. The square law assumes that battles involve concentrated attack, with many members of the more numerous side ganging up on individual opponents. The linear law assumes that battles consist of a series of duels, so that superfluous individuals on the more numerous side remain unengaged until opponents become available. In square-law battles, victory depends mainly on numerical superiority, whereas in linear-law battles, victory depends more strongly on relative fighting value.

Franks & Partridge (1993) were the first to show that Lanchester's theory of combat could be applied to animals other than humans. They predicted that the contrasting patterns of attrition described by the square and linear laws should explain contrasting combat strategies among different ant species. Subsequent experiments with several ant species have supported these predictions (Whitehouse & Jaffe 1996; McGlynn 2000). Here, we re-examine one set of data (Wilson *et al.* 2001) to test whether the willingness of wild chimpanzees (*Pan troglodytes*) to approach a simulated intruder follows the predictions of the square law. We also make predictions based on this model for how chimpanzees should respond to multiple intruders and discuss potential applications of the square and linear laws for understanding combat strategies in other species.

Chimpanzees live in groups of 20–150 individuals and travel in temporary parties of varying size (Goodall 1986; Chapman *et al.* 1994; Watts & Mitani 2001). Males breed in their natal group, defend group territories and sometimes kill members of neighbouring groups. Such killing probably benefits the attackers by reducing the fighting strength of the victim's group. The attackers thereby increase their chances of success in future battles, resulting in increases in territory size, better access to food and females and reduced danger from neighbouring groups (Nishida *et al.* 1985; Goodall 1986; Wrangham 1999; Williams 2000). Females and adolescent males sometimes participate in intergroup encounters, mainly by observing, displaying and vocalizing (Boesch & Boesch-Achermann 2000), but in general only adult males conduct direct physical attacks (Wrangham 1999). We therefore focus on contests between adult males.

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Chimpanzee intergroup fights include both 'gang attacks', in which multiple fighters concentrate attack on a single victim, and 'battles', with multiple opponents on each side (Manson & Wrangham 1991). The square law should be a particularly appropriate model for gang attacks. In gang attacks, some of the attackers immobilize the victim while others beat, bit and otherwise injured the victim (Goodall 1986; Wrangham 1999). The degree to which chimpanzees can concentrate attack during 'battles', contests with multiple fighters on each side (Manson & Wrangham 1991), is less clear (see § 4).

Whether or not the square law applies to chimpanzee battles, the linear law seems an inappropriate model. It assumes lethal duels, which have been observed in many species but not chimpanzees.

In this paper, we seek to draw attention to a theoretical perspective that has long been ignored by biologists, recognizing that future applications may require more sophisticated approaches. For example, even simple Lanchester situations can yield unstable solutions, especially when small numbers of discrete fighting units are involved (McCue 1999).

Chimpanzee intergroup contests appear to satisfy two additional conditions of the square law: (i) that battle is potentially to the death; and (ii) that attack proceeds without recruitment of new combatants. The first condition (i) appears satisfied, in that chimpanzees inflict fatal injuries on foreign males whenever they have the opportunity (Manson & Wrangham 1991). Regarding (ii), recruitment of new combatants may occur in chimpanzee intergroup contests, but observations suggest that such recruitment is rare, probably because distinct parties are typically scattered over a large territory (10–38 km^2 in forest sites (Goodall 1986; Williams 2000; Wilson *et al.* 2001)).

Wilson *et al.* (2001) conducted a series of playback experiments to determine the factors underlying response to the call of a foreign intruder. Intergroup encounters occur with low frequency and are difficult to observe systematically: playback experiments provide an opportunity to collect systematic data appropriate for testing explicit models. In each trial, a single pant-hoot vocalization of a single foreign male was played through a speaker, which was immediately removed so that no chimpanzees saw the speaker in operation. Observers recorded the identity of all individuals in the focal party and any other parties known to be within acoustic range of the speaker. Observers then measured the paths travelled and calculated the latency to 100 m, defined as the time (to the nearest minute) taken by the focal party to travel 100 m towards the speaker. These playbacks elicited cooperative responses, with the nature of the response depending on the number of adult males in the party. Parties with three or more males consistently joined in a chorus of loud vocalizations and approached the speaker together. Parties with fewer adult males usually stayed silent, approached the speaker less often and travelled more slowly if they did approach. To avoid pseudoreplication, we used a single focal party for each trial. Only in one trial (no. 96.01) were latencies measured for multiple focal parties, and the choice of party does not substantially affect the results.

The speed of approach increased with increasing number of males within acoustic range ($n = 15$ trials, $r^2 = 0.52$, $p < 0.005$ or $r^2 = 0.38$, $p < 0.05$, depending on the party used for trial 96.01). Although this linear model provides a reasonably good fit to the data, it predicts a measurable speed for parties with one male (0.5 to 1 km h^{-1} in this case), whereas lone males did not in fact approach the speaker. A model based on the square law should provide a better qualitative fit.

2. LANCHESTER'S SQUARE LAW AND SIMULATED GANG ATTACKS

We postulate that these playback experiments emulate potential gang attacks, which meet the conditions of the square law. The square law assumes that all individuals on both sides are equally vulnerable to attack from every individual on the opposing side and that individuals are killed at a rate proportional to the numbers on the opposing side. The following equations describe the rates of attrition of the two sides:

$$\mathrm{d}m/\mathrm{d}t = -\alpha n, \qquad \mathrm{d}n/\mathrm{d}t = -\beta n, \tag{2.1}$$

where m and n are the numbers of survivors remaining at time t since the start of the battle; α and β are constants representing the relative fighting values of individuals on the two sides. Every individual on the numerically weaker side finds itself the focus of concentrated attack by more than one individual on the opposing side. The disparity between the fighting forces increases through time as the larger side focuses more and more of its attacking strength upon the dwindling opposition. Dividing the two equations to eliminate time and integrating gives:

$$\beta(m_0^2 - m^2) = \alpha(n_0^2 - n^2). \tag{2.2}$$

If the battle continues until all individuals on side n are killed, $n = 0$ and

$$m = (m_0^2 - (\alpha/\beta)n_0^2)^{1/2}, \tag{2.3}$$

where m_0 and n_0 represent the numbers on sides m and n at the start of the battle. For m to win, therefore, $m_0^2 > (\alpha/\beta)n_0^2$, or

$$\beta m_0^2 > \alpha n_0^2. \tag{2.4}$$

Either side of equation (2.4) is proportional to the fighting strengths of one of the two groups. The square terms highlight the relative importance of superior numbers over individual fighting value.

If equation (2.4) holds, the losses incurred by either side are n_0 and $(m_0 - (m_0^2 - (\alpha/\beta)n_0^2)^{1/2})$, respectively.

Following Wrangham (1999), we propose that the primary benefit of entering the contest is killing rivals and the principal cost is the death of coalition members. In doing so, we nevertheless recognize that, like other territorial animals, chimpanzees probably gain multiple benefits from attacking extra-group males, including defence of food and mates as well as protection of self, infants and other group members from attack (Watts & Mitani 2001).

Not all battles between opposing groups of chimpanzees are to the death. In applying the square law to chimpanzees, we shall therefore assume that the expected losses incurred by either side are proportional to—rather than equal to—the losses predicted by the square law, and are δn_0 and $\delta(m_0 - (m_0^2 - (\alpha/\beta)n_0^2)^{1/2})$, respectively, where δ is a constant. We shall neglect any differences (such as asym-

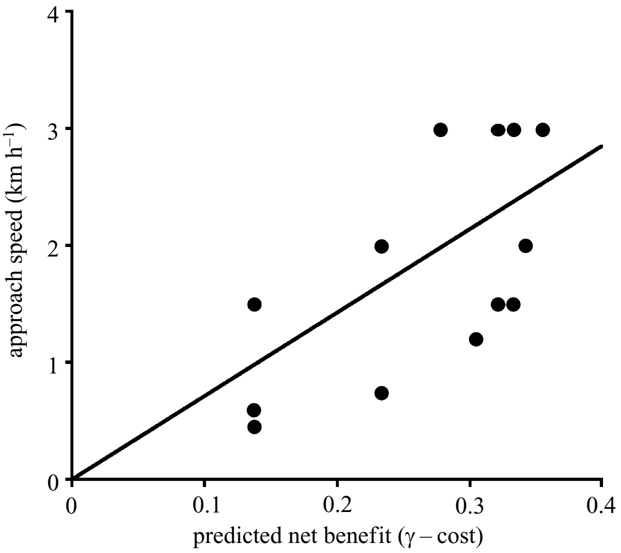

Figure 1. 1 Plot of speed of approach versus the net benefits of attacking as predicted by Lanchester's square law, based on the total number of males in acoustic range. The regression equation is: approach speed = 0.0 + 7.1 (γ − cost), where γ equals the benefit of killing a member of an opposing coalition; $r^2 = 0.42$; $p < 0.01$; $n = 15$ trials.

metries in ownership, e.g. Davies (1978)) between groups and assume that only adult males fight, so that $\alpha = \beta$. Let the cost of losing a coalition member be 1 and the benefit of killing a member of an opposing coalition be γ, where $\gamma < 1$.

The playback experiments simulate one opponent. The expected loss incurred by the opponents is δ, and by the focal group $\delta(M_a - (M_a^2 - 1^2)^{1/2})$, where M_a is the initial number of males within acoustic range.

Using the number of adult males within acoustic range for M_a satisfies the condition of no recruitment. In practice, for all but two of the trials for which latency was measured, the males in the focal party were the only males known to be within acoustic range. The choice of M_a (males in acoustic range or focal party) has little effect on the results.

Hence

$$\begin{aligned}\text{net benefit} &= \text{benefit} - \text{cost}\\ &= \delta(\gamma \times 1 - 1(M_a - (M_a^2 - 1^2)^{1/2})).\end{aligned}$$

We hypothesize that the speed of approach (1/latency time (L)) provides a measure of the propensity to attack and is proportional to expected net benefit.

Hence:

$$1/L = k\delta(\gamma - (M_a - (M_a^2 - 1^2)^{1/2})).$$

$-k\delta$ is the slope and $k\delta\gamma$ is the intercept of the least-squares fit of $1/L$ versus $(M_a - (M_a^2 - 1^2)^{1/2})$.

Hence γ can be determined and a plot of $1/L$ versus $(\delta(M_a - (M_a^2 - 1^2)^{1/2}))$ will be a straight line through the origin (figure 1). This linear relationship fits the data well. A better fit might be obtained with a more complex curve, but the marginal improvement would not justify the additional parameters required.

To test which factors best predicted the speed of approach, we ran backward stepwise logistic regressions with the following independent variables: number of adult males within acoustic range of the speaker, number of adult females in the immediate party and the net benefits predicted by the square law. We used a p-level-to-retain of 0.10. Depending on which party from trial 96.01 was included, the only variable to be retained was either the predicted net benefit ($F_{1,13} = 9.52$, $r^2 = 0.42$, $p < 0.01$) or the number of males within acoustic range ($F_{1,13} = 14.34$, $r^2 = 0.52$, $p < 0.005$).

3. APPLICATION TO BATTLES

Now suppose that there are n_0 opposing males, benefit − cost = $\delta(\gamma n_0 - (M_a - (M_a^2 - n_0^2)^{1/2}))$.

This is zero when $\delta(\gamma n_0 - (M_a - (M_a^2 - n_0^2)^{1/2})) = 0$, which can be solved to give $M_a = ((1 + \gamma^2)/(2\gamma))n_0$.

Calculated as shown above from the slope and intercept of the least-squares fit of $1/L$ versus $(M_a - (M_a^2 - 1^2)^{1/2})$, $\gamma = 0.40$ and thus $M_a = 1.5n_0$. We can therefore predict that, in this population, male chimpanzees should be willing to enter a contest against more than one opponent only if the total number of nearby allies is more than 1.5 times the number in the opposing group.

4. DISCUSSION

Lanchester's square law provides an explicit model for numerical assessment in intergroup contests. Wilson *et al.* (2001) found that male chimpanzees were more likely to approach a simulated intruder—and approached more quickly—the more they outnumbered the intruder. This pattern of approach is consistent with the square law. Here, we show that one measure of willingness to enter an intergroup contest, the speed of approach, increased with increases in the net benefits predicted by a model based on the square law. With the small sample size, we were unable to determine whether the predicted net benefits or the raw number of males present better predicted the speed of approach. Nevertheless, the square-law model has the advantage of explaining rather than merely describing the pattern of approach. Additionally, the square law correctly predicted that lone males should be unwilling to approach.

The square-law model predicts that, for this population, male chimpanzees should be willing to fight a group of foreign males whenever they outnumber their rivals by a factor of 1.5. This result is consistent with the results of the playbacks in which parties with one male did not approach until joined by allies and parties with two males approached in four out of seven cases. In practice, however, wild chimpanzees seem to require at least three males to kill an adult (Wrangham 1999). In support of this, male chimpanzees approaching playbacks did not vocally advertise their presence unless in parties with three or more males (Wilson *et al.* 2001). The quiet approaches by males in smaller groups suggest that they perceived greater risk and/or a lower probability of successful attack. In one case in captivity two males killed another male, but this case may be anomalous in that the confines of a night cage restricted the victim's ability to escape or to recruit allies (de Waal 1989). The low minimum ratio determined here may result from using data from playbacks rather than actual encounters. Although approach to a stranger's call probably correlates with willingness to attack, such an attack is not inevitable. Individuals approaching a stranger's call may be interested simply in a closer look; the presence of at least one ally may reduce risks and make such an inspection worthwhile.

Recent discussions of chimpanzee aggression have focused on gang attacks on solitaries (Manson & Wrangham 1991; Wrangham 1999). The square-law model supports this view and makes a more general prediction: killing should occur whenever the attackers sufficiently outnumber their opponents. In contrast to this prediction, chimpanzee battles rarely result in fatalities or even serious injuries (Goodall 1986; Boesch & Boesch-Achermann 2000). Only one of five killings at Gombe involved a battle (Goodall 1986). Nevertheless, chimpanzee battles remain poorly understood. More observations from sites with neighbouring habituated communities and more detailed analysis of long-term data are needed to determine the relative frequency of opportunities for battles and gang-attacks. Willingness to enter battles could also be tested with playbacks simulating multiple foreign male intruders.

The model used here assumes that the benefit of battle increases with the number of opponents ($\delta\gamma n_0$). Gaining the full benefit would thus require that all opponents be destroyed, something never observed in a single chimpanzee battle. To achieve full destruction, chimpanzees would have to systematically isolate and kill each individual. With their limited weapons (teeth and hands), chimpanzees take tens of minutes to kill an enemy and therefore might be unable to kill multiple opponents—the enemy is likely to escape or regroup before the attackers disable the first victim. Moreover, with their small group sizes and low reproductive rate (Kaplan *et al.* 2000), chimpanzees are probably incapable of inflicting or sustaining the levels of attrition seen in human or insect armies. Although chimpanzee battles may rarely or never result in multiple casualties, the square law nevertheless appears to model accurately the relative costs and benefits of approaching a single rival.

Lanchester's laws of combat aid our understanding of intergroup aggression in humans, ants and chimpanzees, and show promise for wide application to other species. For instance, the laws permit a refinement of the general expectation (e.g. McComb *et al.* 1994) that resource-holding potential depends on individual fighting value in one-on-one contests and relative numbers in intergroup contests.

Apart from social insects, most examples of potentially lethal animal contests appear to be duels fought between individuals (Geist 1975; Wilkinson & Shank 1976; Fossey 1983; Huntingford & Turner 1987; Byers 1997; West *et al.* 2001) or gang attacks (Kruuk 1972; Caro & Collins 1986; Packer *et al.* 1988; Starin 1994; Mech *et al.* 1998). Duels can be considered a special case of the linear law, where $M_0 = n_0 = 1$. In duels, success depends on individual fighting value, as seen by huge investments in body size and weaponry in species in which males fight duels for access to females. By contrast, species with gang attacks seem likely to follow the square law and are hence predicted to show less investment in weaponry. Plavcan *et al.* (1995) found that, among primate species in which the outcome of fights is typically determined by coalitionary fighting, selection for weaponry (canines) is reduced. In particular, male chimpanzees have relatively small canines for their body size, consistent with other evidence that success in battle for chimpanzees depends on coalition size rather than individual weaponry.

In addition to duels and concentrated attacks, some animals may fight linear-law battles, in which groups fight one another in a series of duels. In such species, fighters should be expected to invest in fighting value, as Franks & Partridge (1993) showed for slave-making ants. Linear-law battles appear to be rare, partly because lethal intergroup aggression is rare and partly because such battles require some method of reducing the effectiveness of concentrated attack. Slave-making ants accomplish this by confusing the rival forces with 'propaganda substances' (Franks & Partridge 1993). In at least one vertebrate species, intergroup battles do potentially follow the linear law. In the naked mole-rat (*Heterocephalus glaber*), narrow burrows constrain the battlefront to a small number of individuals on each side. Consistent with the prediction of the linear law, individuals most active in experimentally induced intercolony battles were significantly larger than other members of the colony (Lacey & Sherman 1991).

Detailed observational and experimental work with lions provides an opportunity to test whether Lanchester's square law applies to other species with gang attacks. Both male and female lions are vulnerable to lethal attack, particularly when outnumbered (Packer *et al.* 1988) and larger groups tend to defeat smaller groups (Packer *et al.* 1990; Grinnell *et al.* 1995). Playback experiments have found that both male and female lions approach the roars of simulated same-sex intruders faster the more they outnumber the intruders (McComb *et al.* 1994; Grinnell *et al.* 1995). However, in contrast to the predictions of the square law, defenders sometimes approached even when outnumbered by simulated intruders. For example, females always approached when they had cubs in the pride (McComb *et al.* 1994) and males approached even when outnumbered by a factor of 3 : 1 (Grinnell *et al.* 1995). Willingness to approach also varied with local population density (Heinsohn 1997).

At least four possible explanations exist for the willingness of lions to approach when outnumbered. First, an unknown number of these playbacks violated Lanchester's assumption of no recruitment. McComb *et al.* (1994) state that female lions in groups below the maximum pride size were more likely to roar following playback, and when they did so, in nearly half of the cases they were joined by other pride members. The number of individuals in acoustic range, however, is not explicitly reported. Second, the playback distance for all of the lion experiments (200 m) was shorter than the median playback distance for chimpanzees (300 m), even though natural lion roars can travel much further than chimpanzee pant-hoots (lions: up to 8 km (Schaller 1972); chimpanzees: at least 1–2 km (Reynolds & Reynolds 1965). The lion playbacks therefore might simulate an intruder–defender distance that is shorter for lions and hence more threatening. Third, the square-law model assumes that defenders that fail to challenge an intruder incur no cost, an assumption that may be untrue for chimpanzees. This assumption is almost certainly untrue for lions, especially females defending cubs, or for males, in which any failure to defend their territory against rival males could result in eviction, with complete loss of lifetime reproductive success (Packer *et al.* 1988). Fourth, the decision to enter an intergroup contest probably depends on additional costs and benefits, including asymmetries in ownership (e.g. Davies 1978) and the 'value of the future', which depends on an individual's expectation of future reproductive opportunities (Enquist & Leimar 1990). Lanchester's square law seems most appropriate when numerical assessment is the overriding factor. The population variation revealed by the lion experiments indicates that the particular value of γ for a particular population of chimpanzees may also depend on local ecology and demography.

In summary, male chimpanzees responded to playbacks in a manner consistent with Lanchester's square law. This relatively neglected theoretical perspective shows promise for applications for other cases of animal combat.

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