Lanchester's attrition models and fights among social animals

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Lanchester's models of attrition during warfare have served as the basis for several predictions about conflicts between groups of animals. These models and their extensions describe rates of mortality during battles as functions of the number and fighting abilities of individuals in each group, allowing analysis of the determinants of group strength and of the cumulative numbers of casualties. We propose modifications to Lanchester's models to improve their applicability to social animals. In particular, we suggest that the per-capita mortality rate of a group is a decreasing function of the fighting abilities of its members, that the mortality rate is an increasing function of the number of individuals in both groups, and that there will often be diminishing returns for increasing numerical advantage. Models incorporating these assumptions predict that the ability of social animals to win fights depends less on group size and more on individual prowess than under Lanchester's original models. We discuss how data on casualties can be used to distinguish among alternative attrition models. *Key words:* aggression, Lanchester models, nonlinear dynamics, social animals. *[Behav Ecol 14:719–723 (2003)]*

Many social animals fight in groups in the context of intraspecific or interspecific competition, predation, or social parasitism. Following Franks and Partridge's (1993) suggestion that Lanchester's models of human warfare (Lanchester, 1916; more accessible in its reprinted form, Lanchester, 1956) could serve as the basis for a theory of group fighting in ants, several authors have tested predictions about animal fights that might arise from these models (e.g., Franks and Partridge, 1993, 1994; McGlynn, 2000; Whitehouse and Jaffe, 1996). Lanchester's models describe rates of attrition in two battling armies as functions of the number and fighting abilities of the individuals in each group. Such models indicate properties of group fighting that are not otherwise obvious and are therefore useful in analyzing fighting strategies, determinants of competitive or predatory ability, and the ecological effects of interactions among groups.

Lanchester's models and their extensions (e.g., Epstein, 1997; Hartley, 1995; Karr, 1983) provide a mathematical framework linking assumptions about the circumstances and mechanisms of fighting to the collective effects of fighting for each group. Lanchester (1916) presented two quantitative models. The first assumes that members of the more numerous group can concentrate their attacks on members of their less numerous foes. This gives rise to the "square law," which states that the ability of a group to win escalated contests is proportional to the square of group size but rises only linearly with individual fighting abilities. Lanchester also proposed a second model from which the "linear law" is derived. Under this model, members of the more numerous group are unable to concentrate attacks, and group strength is linearly proportional to both group size and individual fighting ability.

If social animals fight in the open, it may be possible for several members of the larger group to attack an opponent simultaneously. In these circumstances, it is tempting to suggest that Lanchester's square law would apply, and therefore

that collective fighting ability is more sensitive to group size than to individual prowess. The square law has been invoked to explain why predaceous army ants rely on large numbers of workers that are smaller than their prey (Franks and Partridge, 1993), why army ants reproduce by colony fission (Franks and Partridge, 1994), why leaf-cutting ants recruit small workers rather than large soldiers during territorial battles (Whitehouse and Jaffe, 1996), why invasive ants tend to be smaller than noninvasive members of the same genera (McGlynn, 1999), and why ant species with small workers are more successful competitors when they forage in the open rather than in constricted spaces (McGlynn, 2000). Wilson et al. (2002) suggested that Lanchester's laws may have wide application to social vertebrates, and they analyzed battles among chimpanzees as an example.

However, to our knowledge no study on nonhuman animals has tested whether Lanchester's models correctly predict casualties during fights. Furthermore, attempts to test Lanchester's models with data from human warfare generally do not support the square law even where concentrated attacks are possible (e.g., Hartley, 1995). Franks and Partridge's (1993) introduction of Lanchester's models to biology was intended to provide a conceptual framework for the study of fights between animal groups and to emphasize the need for testing and refining the model based on data. We suggest that progress can be made in at least two ways: by determining empirically the relationship between casualty rates during group fights and various explanatory variables, and by development of modifications to Lanchester's models that may make the models more appropriate to social animals. In this paper, we propose several simple modifications and indicate why the particular quantitative models presented by Lanchester are unlikely to apply to social animals without such alterations. We also indicate how empirical studies can distinguish among these possibilities.

Lanchester's square and linear laws as models of animal conflict

In Lanchester's (1916) models, each army is assumed to consist of individuals with equivalent fighting abilities. Because these models do not include recruitment or reinforcement, group sizes decline from their original values. These

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assumptions have been modified in later work (e.g., Hartley, 1995; Karr, 1983).

Lanchester's "square law" arises when two armies fight in such a way that the individuals in one group can concentrate their attacks on opponents. Let m and n equal the number of surviving individuals in groups 1 and 2, respectively. Group sizes at the start of the fight are m_0 and n_0. Let α_m equal the fighting ability of each individual in group 1, and let α_n equal the fighting ability of each individual in group 2. The fighting ability expresses the rate at which an individual can kill opponents within a particular context. Under Lanchester's model, rates of mortality are described by the following pair of equations:

$$dm/dt = -\alpha_n n \qquad dn/dt = -\alpha_m m. \qquad (1)$$

In words, the instantaneous death rate experienced by a fighting group is equal to the product of the number of opponents and their individual fighting abilities. This model has several mechanistic interpretations in the literature on human warfare, which assume that armies are reduced according to the rate of incoming fire from the opposing army (Karr, 1983). Integration leads to the following state equation, which is satisfied at any time during the battle:

$$\alpha_m(m_0^2 - m^2) = \alpha_n(n_0^2 - n^2). \qquad (2)$$

The fighting strength of group 1 is higher (its per capita death rate is lower) when:

$$\alpha_m m_0^2 > \alpha_n n_0^2. \qquad (3)$$

If this inequality is met, then in a fully escalated fight, group 2 will be eliminated, while group 1 still has survivors. Thus, group fighting ability is proportional to the square of the size of the fighting group but is only linearly related to individual fighting ability (Franks and Partridge, 1993; Lanchester, 1916). It is therefore more important to enter battle with a large army than with fighters of high prowess.

Lanchester proposed a second model, from which the linear law is derived. Here there is some possible terminological confusion, because Franks and Partridge (1993) differ from other authors (e.g., Hartley, 1995; Karr, 1983) as to which model underlies the linear law. Also, both models supporting the linear law are based on nonlinear differential equations, whereas the square law is based on linear differential equations. The name of the law refers to the linear relationship between fighting ability and group size apparent in their common state equation. The first linear law model was presented in mathematical form by Lanchester (1916). It assumes that death rates are proportional to the product of the sizes of the two armies.

$$dm/dt = -\alpha_n mn \qquad dn/dt = -\alpha_m mn. \qquad (4)$$

The following state equation is satisfied at any point during the battle:

$$\alpha_m(m_0 - m) = \alpha_n(n_0 - n). \qquad (5)$$

Group 1 has the greater fighting ability and is expected to win a fully escalated fight if

$$\alpha_m m_0 > \alpha_n n_0. \qquad (6)$$

Thus, group strength is equally sensitive to the size of the army and to individual fighting abilities. This model was intended for circumstances in which "there is no direct value in concentration" (Lanchester, 1956: 2148), which can result if it becomes more difficult to acquire a target in the opposing group as the size of the opposing group is reduced (Epstein, 1997; Karr, 1983).

The second linear law model (Franks and Partridge 1993) results from the assumption that all fighting occurs in one-to-one contests, a situation that Lanchester described verbally. The death rates are given by:

$$dm/dt = -\alpha_n \min(m,n) \qquad dn/dt = -\alpha_m \min(m,n). \qquad (7)$$

For both groups, the mortality rates are proportional to the number of survivors in the smaller group, since the excess members of the larger group do not participate until there is an opportunity to replace a member of their own army. This may be true when the geometry of the battlefield does not allow simultaneous attacks of many against one. The state equation and the conditions under which group 1 wins are the same as for Lanchester's model (equations 5 and 6).

Dependence of mortality rates on a group's own size and individual fighting abilities

The models summarized above assume that the death rate suffered by a fighting group is not directly affected by the fighting abilities of its own members. This can be seen by examining expressions 1, 4, and 7. The term representing fighting ability within a group does not appear in the equation describing that group's own death rate. For example, the expression for dm/dt (the death rate of army m) does not include α_m. Fighting abilities affect death rates indirectly because powerful fighters more rapidly erode the size of the opposing group, reducing the killing power directed toward themselves. The rationale for this assumption is that Lanchester (1916) sought to describe the effects of weapons, such as guns or artillery, that are used to fire on opponents. Such weapons are effective offensively but are not used directly in defense because they rarely intercept incoming projectiles. In Lanchester's (1956: 2139) words, "But the defense of modern arms is indirect; tersely, the enemy is prevented from killing you by your killing him first, and the fighting is essentially collective." Yet in fights among animals (and in hand-to-hand human combat), defense is both direct and indirect. Opposing individuals grapple in immediate contact with one another and kill by biting, stinging, striking, dispersing chemicals, or by rupturing the opponent's skin or exoskeleton. It seems highly likely that animals that are better able to inflict injury or death on opponents are also better able to defend themselves from injury. Increased size, strength, weaponry, and skill serve both functions.

Lanchester's square law also assumes that death rates for each group do not depend directly on the number of individuals within the group. Again, the rationale is apparent if one considers human armies firing projectiles. A force of 10 archers may cause as many casualties per minute when they face 100 opponents as when they face 40 opponents, so long as they can acquire targets at the same rate. In contrast, among groups of animals for which fighting requires close contact, death rates should depend on the size of both groups because both variables affect the rate of encounter.

Here we present a more general model that allows for the possibility that a group's attrition rate may be affected by its own size and fighting abilities. We start by rearranging the state equation and introducing two parameters, θ and λ.

$$\frac{(m_0^\theta - m^\theta)}{(n_0^\theta - n^\theta)} = \left(\frac{\alpha_n}{\alpha_m}\right)^\lambda. \qquad (8)$$

Expressions 2 and 5 are special cases. It can readily be shown that equation 8 is implied by the following pair of differential equations:

$$\frac{1}{m}\frac{dm}{dt} = -\frac{\zeta(m, n, \alpha_m, \alpha_n)}{\alpha_m^\lambda m^\theta} \qquad \frac{1}{n}\frac{dn}{dt} = -\frac{\zeta(m, n, \alpha_m, \alpha_n)}{\alpha_n^\lambda n^\theta}, \qquad (9)$$

where $\zeta(m, n, \alpha_m, \alpha_n)$ is any function of the sizes and fighting abilities of the two groups. For Lanchester's linear law (using Lanchester's equations), $\theta = 1.0$, $\lambda = 1.0$, and

$$\zeta(m, n, \alpha_m, \alpha_n) = \alpha_m \alpha_n mn. \qquad (10)$$

For Franks and Partridge's linear law, $\theta = 1.0$, $\lambda = 1.0$, and

$$\zeta(m, n, \alpha_m, \alpha_n) = \alpha_m \alpha_n \min(m, n). \qquad (11)$$

The state equation 8 is identical for these two models, illustrating that the values of θ and λ do not specify a unique attrition model. Under either version of the linear law, the expression on the left-hand side of equation 8 is simply the ratio of the cumulative number of deaths in group 1 to the cumulative number of deaths in group 2, and the expression on the right-hand side of equation 8 is the ratio of individual fighting abilities.

Under Lanchester's square law, $\theta = 2.0$, $\lambda = 1.0$ and

$$\zeta(m, n, \alpha_m, \alpha_n) = \alpha_m \alpha_n mn. \qquad (12)$$

Clearly, the parameters θ and λ can take on other values as well. Substituting equation 12 into equations 9 and rearranging leads to the following:

$$\frac{dm}{dt} = -\frac{\alpha_n}{\alpha_m^{\lambda-1}} m^{2-\theta} n \qquad \frac{dn}{dt} = -\frac{\alpha_m}{\alpha_n^{\lambda-1}} mn^{2-\theta}. \qquad (13)$$

This arrangement helps to clarify that $\lambda - 1$ represents the dependence of a group's mortality rate on the fighting abilities of its members and that $2-\theta$ represents the dependence on the group's own size. If $\lambda > 1.0$, the death rate for each group is a decreasing function of the fighting abilities of its members; if λ is equal to 2.0, then each group's death rate is affected as much by its own members' fighting abilities as by the opponent's. When $\theta < 2.0$, each group's death rate depends directly on its own numbers to some degree; if θ is equal to 1.0, then the sizes of both groups have equal effects.

Equation 8 implies that group 1 has a greater collective fighting ability when

$$\alpha_m^\lambda m_0^\theta > \alpha_n^\lambda n_0^\theta. \qquad (14)$$

Thus, the relative importance of group size and individual fighting ability depends on the values of θ and λ. Figure 1 illustrates the advantage in individual fighting ability that would be needed to overcome an opponent's advantage in numbers for different values of θ and λ. It is possible that the fighting strengths of animal groups are more sensitive to individual abilities than to numbers even when group attacks on individuals are common.

Diminishing returns to increasing numerical advantage

The model producing Lanchester's square law assumes that the mortality rate of a fighting group increases without limit as the size of the opposing force rises. This is unlikely to be true for animals that grapple directly with one another. Animals may be better able to kill opponents when they attack in pairs rather than singly, but if the numerical advantage continues to rise, there may be diminishing returns to the addition of the third, fourth, or tenth individual to the group attacking a single foe.

Lanchester's models can be modified to represent diminishing returns for increasing numerical ratios. Let the following expressions represent the per capita death rate for two fighting groups:

$$\frac{1}{m}\frac{dm}{dt} = -\frac{\alpha_n}{\alpha_m^{\lambda-1}} g\left(\frac{n}{m}\right) \qquad \frac{1}{n}\frac{dn}{dt} = -\frac{\alpha_m}{\alpha_n^{\lambda-1}} g\left(\frac{m}{n}\right), \qquad (15)$$
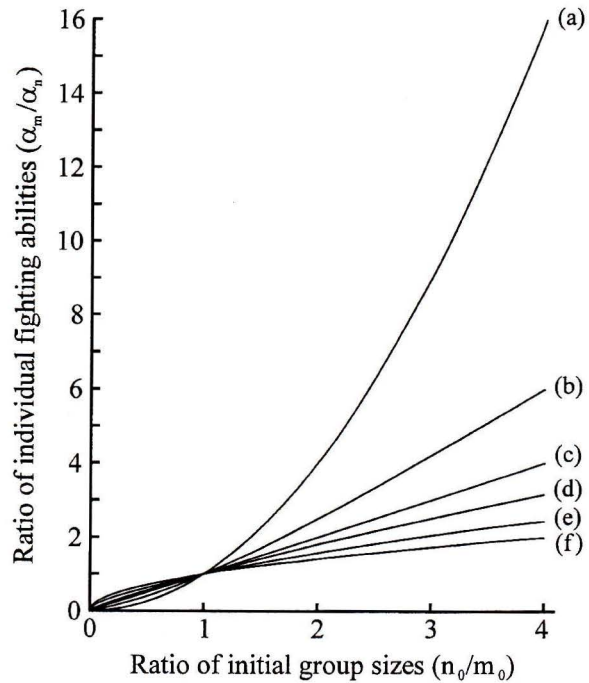

Figure 1
The advantage in individual fighting ability that a group must have (α_m/α_n) to overcome the initial numerical advantage of the opposing group (n_0/m_0). Each curve shows, for a particular type of attrition model, the ratios of fighting abilities and numbers of individuals for which the two groups will have equal strengths, as measured by per-capita rates of mortality or ability to win fully escalated contests. For each model, in the region above the line, group 1 (with individual fighting ability α_m and initial number m_0) will win, and in the region below the line, group 2 (with individual fighting ability α_n and initial number n_0) will win. (a) Lanchester's square law ($\theta = 2.0$, $\lambda = 1.0$); (b) Michaelis-Menten model (equations 15 and 19), $\lambda = 1.0$, $A = 3.0$; (c) Lanchester's linear law ($\theta = 1.0$, $\lambda = 1.0$); (d) Michaelis-Menten model; $\lambda = 2.0$, $A = 6.0$; (e) Michaelis-Menten model; $\lambda = 2.0$, $A = 3.0$; (f) modified Lanchester model (equations 13) with $\theta = 1.0$, $\lambda = 2.0$.

where $g(n/m)$ is an increasing, but decelerating function of numerical ratios. Hence

$$\frac{dm}{dn} = \left(\frac{\alpha_n}{\alpha_m}\right)^\lambda \frac{m}{n} F\left(\frac{m}{n}\right), \qquad (16)$$

where F is defined by

$$F(r) = \frac{g(1/r)}{g(r)}. \qquad (17)$$

Notice that F is decreasing and therefore invertible. Notice also that $m = cn$ is a solution curve if $\alpha_n^\lambda F(c) = \alpha_m^\lambda$, or $c = F^{-1}(\alpha_m^\lambda/\alpha_n^\lambda)$. Furthermore, dm/dt and dn/dt are strictly negative everywhere. So

$$m = F^{-1}(\alpha_m^\lambda/\alpha_n^\lambda)n \qquad (18)$$

defines a separatrix in the n-m plane between solution curves that approach $n = 0$ (so that group 1 wins) and those that approach $m = 0$ (so that group 2 wins).

Suppose, for example, that g takes the Michaelis-Menten form

$$g(r) = Kr/(A + r), \qquad (19)$$

which rises to an asymptotic value of K and which reaches half this value when $r = A$. For example, if $A = 3$, this implies that members of a group attain half of the maximum possible rate of killing of their opponents when they outnumber the opponents 3 to 1. For this functional form,

$$F(r) = \frac{A + r}{r(1 + Ar)}.$$ (20)

Then, Equation 18 implies that group 1 wins if

$$\frac{m_0}{n_0} > \frac{2A\alpha_n^\lambda}{\alpha_m^\lambda - \alpha_n^\lambda + \sqrt{(\alpha_m^\lambda - \alpha_n^\lambda)^2 + 4A^2\alpha_m^\lambda\alpha_n^\lambda}}.$$ (21)

For purposes of determining how great an advantage in individual fighting ability a group must have to overcome a particular numerical disadvantage (Figure 1), inequality 21 can be rearranged to show that for a given ratio of starting numbers (m_0/n_0), group 1 wins if

$$\frac{\alpha_m}{\alpha_n} > \left\{ F\left(\frac{m_0}{n_0}\right) \right\}^{\frac{1}{\lambda}} = \left\{ \frac{n_0(m_0 + An_0)}{m_0(n_0 + Am_0)} \right\}^{\frac{1}{\lambda}}$$ (22)

Figure 1 illustrates how this curve varies for different values of λ and A.

DISCUSSION

Lanchester's attrition models and their extensions predict the relative impact of numbers and of individual killing power on the collective fighting ability of a group. The models provide a means to link assumptions about the mechanisms of fighting to predictions about the patterns of casualties accruing to each group. Early applications of this body of theory to social animals (Franks and Partridge, 1993, 1994) identified a key difference between two types of fights. In the first, members of one group can concentrate attacks on opponents, as assumed by the model producing Lanchester's square law. In the second, opponents engage in a series of one-on-one duels, as in Franks and Partridge's model of the linear law (Franks and Partridge, 1993). According to the original models, group strength is disproportionately sensitive to numbers in the first type of fight, but not in the second.

Our modifications of Lanchester's models indicate a wider range of possible attrition patterns for the same types of fights (Figure 1). We predict that the importance of group size relative to individual fighting ability is most often lower for social animals than for the human armies envisioned by Lanchester, because Lanchester's models assume that death rates during battles are not affected by a group's own individual strengths. The relative importance of group size and individual fighting ability depends on the values of θ and λ (equations 13 and 14). If increased strength and weaponry directly improve an animal's ability to defend itself, as well as to kill opponents, then λ will exceed the value of 1.0 assumed by Lanchester's models. If a group's size affects its own rate of mortality, then θ will be smaller than the value of 2.0 assumed by the square law. Furthermore, if there are diminishing returns for bringing more individuals into attacks of many against one, then the importance of numerical advantage is reduced. Any of these properties of group fights will diminish the importance of group size relative to individual prowess; indeed, group strength may be more sensitive to individual abilities than to numbers (Figure 1, curves e and f).

Empirical studies are needed to test both the assumptions and the predictions of these attrition models. Such studies can determine whether the instantaneous or short-term death rate experienced by a fighting group declines with increasing fighting abilities of its members. For example, in fights between a pair from one group and a single individual from a rival group, is the probability that the first casualty is incurred by the single individual a decreasing function of its own size or weaponry, as assumed by equations 13 with $\lambda > 1.0$, or does it depend only on the fighting abilities of its opponents, as assumed by Lanchester's models? Similarly, does a group's short-term death rate vary with its own group size, as assumed by equations 13 with $\theta < 2.0$, or only with the size of the opposing group, as assumed by the square law?

Empirical studies can also analyze the total casualties accumulating in two fighting groups as a function of the numbers and abilities of individuals in each group. This can be achieved for social insects, many of which engage in large group fights producing many deaths (e.g., Levings and Adams, 1984; Mabelis, 1979), and for which individual fighting abilities can be selected by choosing insects of a particular size or caste. Suppose that worker ants of a specific size are drawn from two different colonies and that worker size is the main determinant of fighting ability. Then all of the terms on the right-hand side of equation 8 are constants. Thus, for the correct the value of θ, the ratio on the left-hand side of equation 8 is expected to be constant or to vary stochastically around a fixed mean, regardless of the initial numbers in the two groups. Since the original numbers, m_0 and n_0, and the numbers of survivors, m and n, are all countable, the value of θ can be estimated by pitting ants from the two groups against one another in different ratios, seeking the value of θ for which the ratio on the left-hand side of equation 8 is most nearly constant. The fit of the model specified by equations 13 can be evaluated further by stochastic simulations (Plowes and Adams, manuscript in preparation).

Lanchester's square law proposes an explanation for why the killing power of a group can be disproportionately sensitive to group size. This sensitivity is due to a compounding effect: even though the instantaneous death rates are linear functions of group size (equation 1), as the battle proceeds, the per-capita death rates accumulate as a function of the square of group sizes (equations 2 and 3). However, there are other possible reasons that group fighting ability might increase faster than linearly with group size. For example, if a pair of fighters coordinate their actions, it is possible that their killing power is greater than twice the killing power of a single fighter. This would occur, for example, if one can immobilize or distract the opponent while the other attacks, so that the opponent is less able to inflict injuries on either of the cooperating fighters. This alternative explanation does not require a compounding effect: the advantages of numbers should apply even during the first death of an opponent. Thus, another approach to testing Lanchester's square law is to compare the ratios of casualties in a series of short fights (e.g., in which there is a single death), to longer fights in which substantial casualties accumulate. If the ratios do not differ, then the square law is not a likely explanation of the patterns of attrition.

Several studies have indicated particular aspects of animal fights that are consistent with Lanchester's square law. We suggest, in agreement with the authors of these studies, that these phenomena have other potential explanations. Lanchester's square law could explain why colonies might produce large numbers of small workers rather than smaller numbers of more massive and powerful fighters. Yet in social insects, worker size and colony size are molded by many selective forces other than escalated battles (e.g., Beshers and Traniello, 1996; Jeanne, 1999), and it is not clear what role patterns of attrition play in shaping worker size. McGlynn's

(1999) comparative study revealed that invasive ant species have significantly smaller body size than other members of the same genera, which could be explained by selection for group fighting ability favoring large numbers of comparatively small workers. However, McGlynn (1999) discusses several alternative explanations in addition to the one suggested by Lanchester's models. The relative foraging success of small and large ants in confined areas (McGlynn, 2000) may be due to differences in the ability to find resources in constricted areas, rather than changes in patterns of mortality during fights. Furthermore, in some species, it has been shown that larger workers or soldiers are particularly likely to participate in fights (e.g., Adams, 1990; Wilson, 1976), contrary to the pattern reported by Whitehouse and Jaffe (1996). Wilson et al. (2002) evaluated the fit of a prediction developed from the square law to the rate at which chimpanzees move toward battles. Although their data reject the null hypothesis of no effect of group size, they did not compare the fit of the data to alternative models assuming lower values of θ, so the square law is not specifically supported. Furthermore, there are other plausible reasons that group fighting ability might be affected disproportionately by numbers. In short, evidence for the square law is equivocal, and published data from nonhuman animals do not yet allow quantitative evaluation of alternative attrition models.

Mathematical models that accurately describe casualties during battles are of obvious utility for the analysis of the behavior, ecology, and evolution of group aggression. However, it is worth emphasizing that these are not complete models of competition or other group interactions, for several reasons. First, not all struggles among social groups take the form of lethal combat. Ants may win competitive struggles by finding food more rapidly and removing it before discovery by other colonies (exploitation, e.g., Wehner, 1987), by foraging at temperatures that other species cannot tolerate (e.g., Adams and Traniello, 1981), or by preventing other colonies from foraging them within their nests (e.g., Möglich and Alpert, 1979). Second, many animals can assess the probable results of battles without engaging in fully escalated fights. This allows the probable loser to withdraw at low cost (Parker, 1974). Some social animals make assessments of opponents that are based in part on relative group size, so that they are less likely to attack when strongly outnumbered (Adams, 1990; Hölldobler, 1981; McComb et al., 1994). In these cases, the expected costs of escalated battle are an important determinant of victory, but these costs are not actually incurred. Third, Lanchester's models represent the costs of battles but not the benefits. Opponents may differ not only in their ability to inflict injuries, but also in the relative value placed on the object of the battle. Evolutionary game theory provides a well-developed framework for analyzing contests between opponents that differ both in fighting ability and in perceived resource value (Dugatkin and Reeve, 1998; Maynard Smith, 1982; Mesterton-Gibbons, 2001; Mesterton-Gibbons and Adams, 1998). A well tested attrition model can provide an important component of the strategic analysis of battles between social groups.

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