# 3 Fights Among Ants and Other Social Animals

The Lanchestrian models in Lecture 2 assume that the death rate suffered by a fighting group is not directly affected by the fighting abilities of its own members—the parameter representing a group's fighting ability within a group does not appear in the equation for that group's own death rate. Rather, 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.[1] Yet in fights among animals—and in hand-to-hand human combat—defense is both direct and indirect. Opponents grapple with one another and kill by biting, stinging, striking, dispersing chemicals or rupturing the opponent's skin or exoskeleton. That animals better able to inflict injury or death on opponents are also better able to defend themselves from injury seems highly likely. 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, as 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.

Accordingly, to model fights among social animals, Adams and Mesterton-Gibbons (2003) developed a more general model, allowing a group's per capita death rate or attrition rate to be affected by both its own size and its fighting abilities:

$$\frac{1}{m}\frac{dm}{dt} = -\frac{\zeta(m, n, \alpha_n, \alpha_m)}{\alpha_m^\lambda m^\theta} \tag{3.1a}$$

$$\frac{1}{n}\frac{dn}{dt} = -\frac{\zeta(m, n, \alpha_n, \alpha_m)}{\alpha_n^\lambda n^\theta} \tag{3.1b}$$

where $\zeta(m, n, \alpha_n, \alpha_m)$ may depend in any way on the sizes and fighting abilities of the two groups. Because $\alpha_m^\lambda m^{\theta-1}\, dm = \alpha_n^\lambda n^{\theta-1}\, dn$, (3.1) is readily integrated to yield the state

[1] In his own 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" (Lanchester, 1956, p. 2139).

equation

$$\frac{m_0^\theta - m^\theta}{n_0^\theta - n^\theta} = \left(\frac{\alpha_n}{\alpha_m}\right)^\lambda \tag{3.2a}$$

or

$$\alpha_m^\lambda\, m_0^\theta + \alpha_n^\lambda\, n^\theta = \alpha_n^\lambda\, n_0^\theta + \alpha_m^\lambda\, m^\theta \tag{3.2b}$$

which is more general than (2.3) or (2.13). Lanchester's models both correspond to

$$\zeta(m, n, \alpha_n, \alpha_m) = \alpha_n \alpha_m m n \tag{3.3}$$

with $\lambda = 1$, but $\theta = 1$ yields his linear law whereas $\theta = 2$ yields his square law. The alternative attritional model (2.23) corresponds to

$$\zeta(m, n, \alpha_n, \alpha_m) = \alpha_n \alpha_m \min(m, n) \tag{3.4}$$

with $\lambda = \theta = 1$. Regardless of whether the model yielding the linear law is (2.11) or (2.23), in either case we have $\lambda = \theta = 1$, and so the expression on the left-hand side of (3.2a) is simply the ratio of the cumulative number of deaths in Group 1 to the cumulative number of deaths in Group 2, while the expression on the right-hand side is the ratio of individual fighting abilities.

Although in principle $\zeta$ is totally arbitrary, in practice $\zeta(m, n, \alpha_n, \alpha_m) = \alpha_n \alpha_m m n$ is a perfectly natural choice (yielding both of Lanchester's models). Substituting from (3.3) into (3.1) and rearranging now yields

$$\frac{dm}{dt} = -\frac{\alpha_n}{\alpha_m^{\lambda-1}} m^{2-\theta}\, n \tag{3.5a}$$

$$\frac{dn}{dt} = -\frac{\alpha_m}{\alpha_n^{\lambda-1}} m\, n^{2-\theta} \tag{3.5b}$$

or

$$-\frac{1}{m}\frac{dm}{dt} = \frac{\alpha_n}{\alpha_m^{\lambda-1}} m^{1-\theta}\, n \tag{3.6a}$$

$$-\frac{1}{n}\frac{dn}{dt} = \frac{\alpha_m}{\alpha_n^{\lambda-1}} m\, n^{1-\theta} \tag{3.6b}$$

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

In these more general circumstances, Group 1 has greater collective fighting ability if

$$\alpha_m^\lambda\, m_0^\theta > \alpha_n^\lambda\, n_0^\theta, \tag{3.7}$$

because then (3.2b) implies $\alpha_n^\lambda\, n^\theta < \alpha_m^\lambda\, m^\theta$ and (2.7) follows from (3.5) in the usual way. Thus, the relative importance of group size and individual fighting ability depends on the values of $\theta$ and $\lambda$, with Group 1 winning when

$$\frac{\alpha_m}{\alpha_n} \;>\; \left(\frac{n_0}{m_0}\right)^{\frac{\theta}{\lambda}}. \tag{3.8}$$

The green curves in Figure 3.1 illustrate the advantage in individual fighting ability that would be needed to overcome an opponent's advantage in numbers for different values of $\theta$ and $\lambda$. It now becomes 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.

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, then there may be diminishing returns to the addition of the third, fourth, or tenth individual to the group attacking a single foe.

We can modify (3.6) for diminishing returns to increasing numerical advantage by substituting $g(n/m)$ for $m^{1-\theta}\, n$, where $g$ increases but decelerates, that is, $g' > 0, g'' < 0$. We obtain

$$\frac{1}{m}\frac{dm}{dt} \;=\; -\frac{\alpha_n}{\alpha_m^{\lambda-1}}\, g(n/m) \tag{3.9a}$$

$$\frac{1}{n}\frac{dn}{dt} \;=\; -\frac{\alpha_m}{\alpha_n^{\lambda-1}}\, g(m/n) \tag{3.9b}$$

and hence

$$\frac{dm}{dn} \;=\; \left(\frac{\alpha_n}{\alpha_m}\right)^{\lambda} \frac{m}{n}\, F(m/n) \tag{3.10}$$

with $F$ defined by

$$F(r) \;=\; \frac{g(1/r)}{g(r)} \tag{3.11}$$

Note that $F$ is decreasing and therefore invertible, and that $m = cn$ is a solution to (3.10) if $\alpha_n^\lambda\, F(c) = \alpha_m^\lambda$ or $c = F^{-1}(\alpha_m^\lambda/\alpha_n^\lambda)$. Moreover, $dm/dt$ and $dn/dt$ are strictly negative. So

$$m \;=\; F^{-1}(\alpha_m^\lambda/\alpha_n^\lambda)\, n \tag{3.12}$$

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), as illustrated by Figure 3.2. In other words, Group 1 wins if

$$m_0 \;>\; F^{-1}(\alpha_m^\lambda/\alpha_n^\lambda)\, n_0 \tag{3.13}$$

or

$$\frac{\alpha_m}{\alpha_n} \;>\; \left\{F\left(\frac{m_0}{n_0}\right)\right\}^{\frac{1}{\lambda}} \tag{3.14}$$

Figure 3.1: The advantage $\alpha_m/\alpha_n$ in individual fighting ability that a group must have to overcome the initial numerical advantage $n_0/m_0$ of the opposing group. Each curve shows, for a given 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 curve, Group 1 (with individual fighting ability $\alpha_m$ and initial size $m_0$) will win; and in the region below the curve, Group 2 (with individual fighting ability $\alpha_n$ and initial size $n_0$) will win. (a) Lanchester's square law; (b) Michaelis-Menten model, $\lambda = 1$, $A = 3$; (c) Lanchester's linear law; (d) Michaelis-Menten model, $\lambda = 2$, $A = 6$; (e) Michaelis-Menten model, $\lambda = 2$, $A = 3$; (f) modified Lanchester model, (3.6) with $\theta = 1$, $\lambda = 2$. The green curves are based on (3.8), the red curves on (3.20).

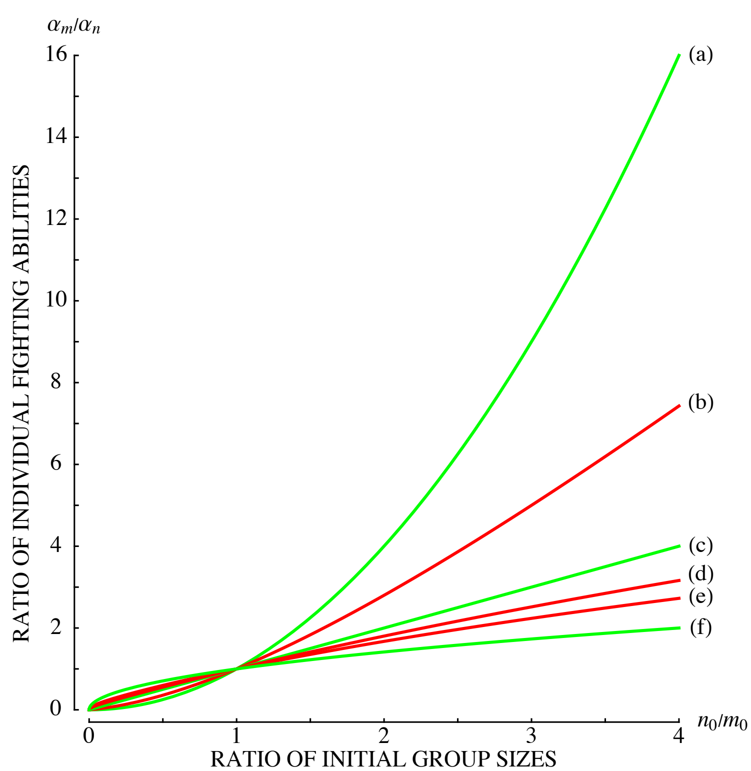
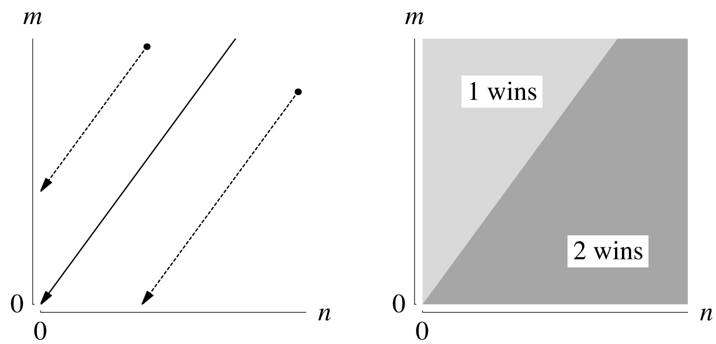


Figure 3.2: Division of $n$-$m$ plane into initial size pairs from which Group 1 wins (light shading) and Group 2 wins (dark shading).




whereas Group 2 wins if $m_0 < F^{-1}(\alpha_m^\lambda/\alpha_n^\lambda)\, n_0$ or (3.14) is reversed.

Suppose, for example, that we take

$$g(r) \;=\; r^{1-p} \tag{3.15}$$

where $0 < p < 1$, so that $F(r) = r^{2p-2}$. Then (3.13) implies that Group 1 wins if

$$m_0 \;>\; \left(\frac{\alpha_m}{\alpha_n}\right)^{\frac{\lambda}{2p-2}} n_0, \tag{3.16}$$

(reducing to the case of Lanchester's square law for $\lambda = 1$ in the limit as $p \to 0$).

In practice, however, we expect that returns to increasing numerical advantage are not only diminishing but also bounded, or $g(\infty) < \infty$. Thus a better choice for $g$ than (3.15) is surely the Michaelis-Menten form

$$g(r) \;=\; \frac{Kr}{A+r} \tag{3.17}$$

for which

$$F(r) \;=\; \frac{A+r}{r(1+Ar)} \tag{3.18}$$

by (3.11); note that $g(r)$ rises to an asymptotic value of $K$, reaching half this value when $r = A$. Then (3.13)–(3.14) imply that Group 1 wins if

$$m_0 \;>\; \frac{2A\alpha_n^\lambda}{\alpha_m^\lambda - \alpha_n^\lambda + \sqrt{(\alpha_m^\lambda - \alpha_n^\lambda)^2 + 4A^2\alpha_m^\lambda\alpha_n^\lambda}}\, n_0 \tag{3.19}$$

or

$$\frac{\alpha_m}{\alpha_n} \;>\; \left\{\frac{n_0(m_0 + An_0)}{m_0(n_0 + Am_0)}\right\}^{\frac{1}{\lambda}}. \tag{3.20}$$

The red curves in Figure 3.1 illustrate (3.20) for different values of $\lambda$ and A.

Lanchestrian models predict the relative impact of numbers and of individual killing power on the collective fighting ability of a group and thus provide a means to link assumptions about the mechanisms of fighting to predictions about the patterns of casualties accruing to each group. As briefly mentioned at the end of Lecture 2, 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 Lanchester's first model. In the second, opponents engage in a series of one-on-one duels, as in the second of the two linear-law models we described in Lecture 2. According to these models, group strength is disproportionately sensitive to numbers in the first type of fight, but not in the second.

Our modified Lanchestrian models show a wider range of possible attrition patterns for the same types of fights (Figure 3.1). 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 $\lambda$ and $\theta$. If increased strength and weaponry directly improve an animal's ability to defend itself, as well as to kill opponents, then $\lambda$ will exceed the value of 1 assumed by Lanchester's models. If a group's size affects its own rate of mortality, then $\theta$ will be smaller than the value of 2 assumed for 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 3.1, curves e and f).