

An empirical test of Lanchester's square law: mortality during battles of the fire ant *Solenopsis invicta*

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Lanchester's models of attrition describe casualty rates during battles between groups as functions of the numbers of individuals and their fighting abilities. Originally developed to describe human warfare, Lanchester's square law has been hypothesized to apply broadly to social animals as well, with important consequences for their aggressive behaviour and social structure. According to the square law, the fighting ability of a group is proportional to the square of the number of individuals, but rises only linearly with fighting ability of individuals within the group. By analyzing mortality rates of fire ants (*Solenopsis invicta*) fighting in different numerical ratios, we provide the first quantitative test of Lanchester's model for a non-human animal. Casualty rates of fire ants were not consistent with the square law; instead, group fighting ability was an approximately linear function of group size. This implies that the relative numbers of casualties incurred by two fighting groups are not strongly affected by relative group sizes and that battles do not disproportionately favour group size over individual prowess.

Keywords: aggression; Bayesian statistics; Lanchester's square law; social animals; *Solenopsis invicta*

1. INTRODUCTION

Many social animals fight in groups, incurring substantial mortality (Hölldobler & Wilson 1990; Wilson *et al.* 2002). Several studies have proposed that Lanchester's (1916) models of human combat may describe conflicts among social animals, including vertebrates and insects (Franks & Partridge 1993; Whitehouse & Jaffe 1996; McGlynn 2000; Wilson *et al.* 2002). Lanchester's models describe casualty rates in two opposing armies as functions of the numbers and fighting ability of individuals on both sides. A well tested model of attrition during fights among social animals would be useful in understanding the evolution of aggressive behaviour, with implications for the mode of colony reproduction (Franks & Partridge 1994), body size (Franks & Partridge 1993; McGlynn 1999), and the ability of introduced species to invade new habitats (McGlynn 1999). However, to our knowledge no previous study has quantitatively tested Lanchester's models for non-human animals.

Lanchester (1916) derived two quantitative laws of combat. The 'square law' applies to circumstances in which members of a larger group can concentrate attacks on members of a smaller group. Lanchester's analysis showed that, under these circumstances, the fighting ability of the group is proportional to the square of the number of combatants but rises only linearly with their individual fighting abilities. If this model correctly describes casualty rates, then the square law has profound consequences for battle tactics (Whitehouse & Jaffe 1996; Adams & Mesterton-Gibbons 2003). Because social animals often gang up on less numerous foes during fights (e.g. Wilson 1975; Heinsohn 1997), it has been

hypothesized that the square law applies broadly to social animals (Franks & Partridge 1993; Wilson *et al.* 2002).

Lanchester's (1916) second quantitative law, the 'linear law', applies to cases in which members of a large group do not concentrate attacks on members of a smaller group. Group fighting ability then rises linearly with group size and individual ability; hence, there is no disproportionate effect of numbers of combatants on ability to win battles. A related model, in which combatants can fight only in one-on-one duels, has similar properties (Franks & Partridge 1993).

The models producing Lanchester's square and linear laws are special cases of a more general model in which the dependence of a group's fighting ability on its own numbers is specified by a single parameter, represented by θ (Adams & Mesterton-Gibbons 2003). Under the square law, θ has a value of 2, whereas under the linear law, the value is 1. Adams & Mesterton-Gibbons (2003) suggested that the square law is unlikely to apply to social animals because it assumes that the mortality rate suffered by a fighting group does not depend on the quantity or individual fighting abilities of its own members. When the model is modified so that each group's mortality rate is affected by its own numbers, this implies that the value of θ is less than 2, and therefore that the importance of group size is reduced relative to individual prowess.

In this study, we used counts of casualties during battles among territorial ants to estimate the value of θ . Workers of the monogyne (single queen) form of the fire ant *Solenopsis invicta* fight in groups, with lethal results, during defence of territory or food resources (Wilson *et al.* 1971; Morrison 2000). In replicated experiments, workers of particular sizes from neighbouring colonies were mixed in different ratios of initial numbers. Ants were placed in containers to prevent withdrawal or recruitment of new

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individuals, thus focusing on mortality as the only cause of changes in numbers. We used Bayesian statistical analysis of death rates to estimate the parameter θ of the generalized Lanchester model.

2. MATERIAL AND METHODS

(a) *The generalized model*

Adams & Mesterton-Gibbons (2003) showed that the models producing Lanchester's linear and square law are special cases of a more general model, in which the death rates are given by

$$\left. \begin{aligned} \frac{dm}{dt} &= -\alpha_m^{(1-\lambda)} \alpha_n m^{(2-\theta)} n, \\ \frac{dn}{dt} &= -\alpha_m \alpha_n^{(1-\lambda)} m n^{(2-\theta)}. \end{aligned} \right\} \quad (2.1)$$

Here, m is the number of survivors in the first group at a given time and α_m is their individual fighting ability; n is the number of survivors in the second group and α_n is their individual fighting ability; t is time. θ and λ parameterize the dependence of a group's fighting ability on its own numbers and individual fighting abilities respectively. The first group has the greater fighting ability if and only if $\alpha_m^\lambda m^\theta > \alpha_n^\lambda n^\theta$. The group with the greater fighting ability has the lower *per capita* death rate and will eliminate the other group in a fully escalated fight. For Lanchester's square law, $\theta=2.0$; thus, the fighting ability of the group rises as the square of its numbers. For Lanchester's linear law, $\theta=1.0$; thus, group fighting ability rises only linearly with numbers. For both of these models, $\lambda=1.0$; however, other values are possible for either parameter (Adams & Mesterton-Gibbons 2003).

At any time during the battle, the following equality is met:

$$R = \frac{(m_0^\theta - m^\theta)}{(n_0^\theta - n^\theta)} = \left(\frac{\alpha_n}{\alpha_m} \right)^\lambda, \quad (2.2)$$

where m_0 and n_0 are the initial numbers of individuals within a group. Notice that for any battle between two homogenous groups, the terms on the right-hand side of equation (2.2) are constants. The original numbers, m_0 and n_0 , and the numbers of survivors when the battle is terminated, m and n , are all countable. Thus, letting $R = (\alpha_n/\alpha_m)^\lambda$, a measure of relative individual fighting ability, there are only two quantities to estimate: θ and R .

(b) *Experimental methods*

(i) *Study site and species*

Our study used ants from monogynous *S. invicta* colonies, which defend exclusive foraging territories (Adams 1998, 2003). Foraging ants were collected in an open pasture near Tallahassee FL, between June and October of 2001. For a more complete description of the study site, see Tschinkel *et al.* (1995). Neighbouring colonies were identified by baiting to a shared territory boundary (Tschinkel *et al.* 1995). Four pairs of colonies with consistently high rates of fighting were used to stage battles.

(ii) *Preparation for battle*

Approximately 10 g of ants were collected per colony from baits placed within the foraging territory. Ants were separated into three size classes, based on head width, using brass sieves. Sieves were nested vertically, with the largest gauge on top and the smallest gauge on the bottom. When ants were placed in the top sieve, they attempted to travel downward through the column of sieves, accumulating at the lowest level

they could reach. The walls of the sieves were coated in Fluon (Northern Products Incorporated, Woonsocket, Rhode Island), which forms a slippery surface, so that ants could not climb to higher levels. The sides were tapped occasionally to excite the ants and expedite movement through the column. Separation was considered complete when all the ants at each level appeared to be homogeneous in size. This was confirmed by subsequent measurements of head width (Porter 1983). The range of head widths was 0.5–0.71 mm for the small size class, 0.71–0.85 mm for the medium size class, and 0.85–1.0 mm for the largest size class.

Ants were marked with fluorescent dye (Markall Ball Paint Marker 1996 LA-CO Industries) so that the colony identities of dead ants could be determined. A pump aerosol was used to spray ants with a solution consisting of 25 ml of ether with 0.5 ml of dye. The quantity of ether was not sufficient to induce narcosis in the ants. For each battle, the two colonies were marked with dyes that differed in colour under ultraviolet light. After the dye solutions had dried, healthy, active ants were chosen.

Each battle arena consisted of a plastic cup, 5 cm high and with a 5 cm diameter base, with Fluon-coated sides. The arena was lined with a 1 cm layer of hardened, water saturated plaster. Battles were initiated within 24 h of the start of collection. After 24 h in a humidified 26 °C insectary, dead ants were removed from arenas and observed under ultraviolet light to determine the number and colony identity of casualties.

(c) *Experimental design*

Four pairs of colonies were used. Depending on the availability of the different sizes of ants, workers from each colony pair were pitted against one another in the following combinations of sizes: medium versus medium, medium versus small, and medium versus large. For each size pairing, ants were fought in numerical ratios of 1 : 1, 1 : 4 and 4 : 1 (except A large versus B medium, fought 1 : 1 and 1 : 5), with total numbers of 50, 100, or 120 ants per arena. Controls containing 100 ants of a single colony were monitored simultaneously. Each treatment and control was replicated two or three times per colony pair, according to the number of available ants.

(d) *Analytical methods*

Bayesian statistical inference was used to estimate θ , the exponent describing the dependence of group fighting ability on numbers, and of R , a measure of relative individual fighting abilities (see equation (2.2)), for each set of replicated battles. Bayesian inference combines prior probability distributions (priors) for each unknown parameter with likelihood functions to yield posterior probability distributions for quantities of interest (Gill 2002; Gelman *et al.* 2004). In essence, the analysis uses the data to move from a state of great uncertainty about parameter values to a state of greater certainty, described by the posterior probability distributions. As data accumulate, the influence of the priors on the posterior inferences diminishes. Summaries of the posterior distributions have straightforward interpretations; for example, the 95% credibility interval contains the true value of the parameter with $p=0.95$, given the data and the model. The study was not designed to estimate λ , which is a component of R .

Since we had little prior information that could guide parameter estimates, we used diffuse prior distributions with

Table 1. Original group size, mean final size and mean % mortality after 24 h of fighting. *N* is the number of replicated battles for each set of conditions. Individuals in each group are of small, medium or large size as indicated.

colony and size of ants	mean group size				mean % mortality		<i>N</i>
	initial		final				
A medium versus B small	A ₀	B ₀	A _t	B _t	A	B	
	50	50	31	12	38	75	3
	10	40	2	33	80	17	3
	40	10	37	6	8	43	3
A large versus B medium	50	50	35	47	30	7	3
	20	100	0	96	100	4	3
A small versus B medium	50	50	15	45	71	11	3
	10	40	0	26	100	4	2
	40	10	30	7	24	27	2
G medium versus Y medium	G ₀	Y ₀	G _t	Y _t	G	Y	
	50	50	11	32	77	37	3
	20	80	3	74	87	7	3
G medium versus Y small	80	20	65	0	19	100	3
	50	50	22	33	57	35	3
	20	80	1	75	97	7	3
J medium versus I medium	80	20	65	16	18	20	3
	J ₀	I ₀	J _t	I _t	J	I	
	50	50	28	4	44	92	3
J medium versus I small	20	80	6	59	70	27	2
	80	20	75	2	6	93	2
	50	50	44	3	11	94	3
U medium versus W medium	20	80	7	21	65	73	3
	80	20	78	1	3	93	3
	U ₀	W ₀	U _t	W _t	U	W	
U medium versus W small	50	50	34	18	32	63	3
	20	80	16	63	22	21	3
	80	20	75	51	7	72	3
U medium versus W small	50	50	49	43	1	10	3
	20	80	19	78	3	14	3
	80	20	79	18	3	3	3

large variances so that plausible values had nearly equally likely prior probabilities. The parameter θ was assigned a normal prior probability distribution with $\mu=2.0$ and $\sigma^2=10^4$. Centring this distribution on the value 2.0 prevents biasing the inferences away from the predictions of the square law. R was assigned a log-normal prior probability distribution with $\mu=0$ and $\sigma=10^2$. Thus, R must have a positive value, and the prior probability of any particular ratio of fighting abilities is equal to the prior probability of its reciprocal. The sensitivity of the inferences to the choice of priors was evaluated *post facto* by running the analyses with different values of μ and σ for each of the prior probability distributions.

A closed form expression for the likelihood function is not available. Therefore, given possible values of θ and R , the likelihood was estimated by simulation. For each battle and pair of parameter values, 10 000 simulations were conducted starting with the observed initial numbers in each group. Notice that equations (2.1) can be rewritten as:

$$\left. \begin{aligned} \frac{dm}{dt} &= -Rcm^{(2-\theta)}n, \\ \frac{dn}{dt} &= -cmn^{(2-\theta)}, \end{aligned} \right\} \quad (2.3)$$

where c is a constant. Thus, the probability that the next death occurs in the first group, given the current number of survivors in the two groups, is:

$$Rm^{(2-\theta)}n/[Rm^{(2-\theta)}n + mn^{(2-\theta)}]. \quad (2.4)$$

For each step of the simulation, a number was drawn randomly between 0 and 1. If the number was less than the value of expression (2.4), then the size of group 1 was reduced by one; otherwise, the size of group 2 was reduced by 1. This was repeated until $m+n$ was equal to the sum of the observed number of survivors at the end of the battle, or until one group was completely eliminated. The proportion of simulations in which the final number of survivors in each group was within one of the observed number (to allow for occasional inaccuracies in identifying the dead) was used as the estimate of the probability of obtaining the observed data for that battle. The likelihood was estimated by the product of these probabilities for all battles for a pair of colonies involving workers of the same size. For example, three contests were conducted between medium sized workers from colony A and small workers from colony B (table 1). Given particular values of θ and R , the likelihood was the product, across all three battles, of the proportion of

Table 2. Estimated values of θ , which quantifies the dependence of group fighting ability on group size, and of R , relative individual fighting ability (with 95% credibility intervals) for specific combinations of colonies and worker sizes (small, medium, or large).

first colony	second colony	θ	R
A medium	B small	1.23 (0.95–1.53)	0.63 (0.47–0.83)
A large	B medium	1.06 (0.54–1.54)	5.50 (2.16–13.1)
A small	B medium	0.71 (0.23–1.10)	5.78 (3.65–8.97)
G medium	Y medium	1.35 (1.17–1.54)	1.74 (1.36–2.21)
G medium	Y small	1.04 (0.82–1.25)	2.29 (1.72–3.04)
J medium	I medium	1.16 (0.94–1.39)	0.49 (0.38–0.63)
J medium	I small	1.31 (1.07–1.59)	0.15 (0.10–0.20)
U medium	W medium	0.73 (0.45–1.00)	0.40 (0.28–0.53)
U medium	W small	0.78 (–1.9 to 3.6)	0.08 (0.0012–0.35)

simulations that yielded the observed number of survivors in each group (± 1).

The likelihood estimates and other steps of the Bayesian analysis were implemented with a programme written in DELPHI 7.0 (Borland International). The Metropolis algorithm, a Markov Chain Monte Carlo (MCMC) method (Gill 2002; Gelman *et al.* 2004) was used to estimate the posterior distribution of θ and R . MCMC methods approximate the posterior probability distributions by simulating large samples from those distributions. For detailed explanations of the Metropolis algorithm and other aspects of MCMC techniques see Chib & Greenberg (1995) and Gill (2002). Here, we briefly summarize the specifications used. When using the Metropolis algorithm, greatest efficiency is achieved if the overall acceptance rate of newly proposed values is in the range of approximately 0.25–0.5 (Chib & Greenberg 1995). Therefore, proposed new values for each parameter were chosen randomly from normal distributions centred on the current estimates with variances selected to achieve a proposal acceptance rate of approximately 0.35.

Use of MCMC techniques requires care to ensure that the Markov chains have converged to the target distribution (Gill 2002). A burn-in or de-memorization period of 1500 steps was discarded from each Markov chain. The remaining values were thinned to 1 in 10 or 1 in 20 as needed to reduce autocorrelations between successive estimates to less than 0.2 for both parameters. For each analysis, five chains were run starting from overdispersed initial values and 1000 values were collected following thinning and after omitting the de-memorization sequence. Visual inspection of trace-plots was used to verify that the burn-in was of sufficient length. Gelman–Rubin diagnostics for each parameter were close to 1.0, as expected if the Markov chains converged to the posterior probability distribution and mixed thoroughly within in (Gill 2002).

3. RESULTS

When ants were placed in the battle arenas, they immediately responded aggressively towards their opponents. Individuals attempted to sever antennae and limbs, or to sting one another. Both pairs and small groups, most often trios, of grappling ants were observed.

In battles among non-nestmates, an average of 42% of the ants died or were fatally injured, but the proportion varied among colonies from 1 to 100% (table 1). Controls incurred 0–1% mortality, with a mean of 0.6%.

The mean value of the estimates of θ was 1.04. The posterior mean of θ for individual colony pairs ranged

from 0.71 to 1.35 (table 2). The 95% credibility intervals lie well below the value of 2 required by the square law except for one set of battles. The exception came during battles between medium-size workers from colony U and small workers from colony W. Few deaths occurred during battles for this set of replicates; therefore, the results yield little information about the value of θ and the 95% credibility interval is very wide (table 1). For two other sets of battles, the credibility interval did not extend as low as 1.0.

Comparison of replicated Markov chains indicated that the estimates of posterior means listed in table 2 are accurate to within approximately 0.02. When the analyses were repeated using different values of μ and σ in the prior specifications (e.g. $\mu=1$ and $\sigma=10^6$), changes in the posterior probabilities of θ were negligible, except for the last set of battles (medium-size workers from colony U versus small workers from colony W). For example, regardless of whether the mean of the prior probability distribution for θ is set to 1.0 or 2.0 for the first set of battles (medium size workers from colony A versus small workers from colony B), the 95% credibility interval for θ ranged from 0.95 to 1.53. Thus, the estimates of θ are determined mostly by the data, through the likelihood function, rather than by the priors.

Although the focus was on estimates of θ , the analysis also yields estimates of R , the relative fighting abilities of workers, for each pair of colonies (table 2). The value of R is less than 1 if the second colony has the lower fighting ability. In the six sets of trials using different sizes of ants, four showed the smaller opponents to have a lower fighting ability (table 2). For two pairs of colonies, the smaller workers had the greater fighting ability (small workers from colony A versus medium workers from colony B, medium workers from colony G versus small workers from colony Y). Of the three same size matches (medium versus medium), the value of R varied from 0.4 to 1.74.

4. DISCUSSION

The results show that for *S. invicta*, θ , which quantifies the sensitivity of group fighting ability to numbers, is approximately equal to 1, well below the value of 2 required by the square law. Thus, Lanchester's square law does not apply to battles among colonies of this species of ant. The estimated values of θ cluster around 1.0 (table 2), the value for which there is no disproportionate effect of numbers on group fighting ability. When θ equals 1, casualty ratios are independent of the ratio of group sizes,

implying that as numerical advantage increases, members of the (numerically) larger group do not achieve a greater concentration of attacks against opponents, or that increased concentration does not affect the casualty ratio. Estimates of θ varied across the experiments and the 95% credibility intervals for two of the data sets do not extend as low as 1.0. Therefore, group fighting ability may be disproportionately affected by numbers for some pairs of colonies, but to a much lower degree than predicted by the square law. By and large, battles among *S. invicta* colonies do not favour group size over individual prowess.

Several analyses of human combat have also failed to support Lanchester's square law (Hartley 1995; Hartley & Helmbold 1995; Friker 1997; Lukas & Turkes 2004). It is easier to estimate attrition models for ants than humans for several reasons. First, there are fewer variables affecting mortality rates in battles among non-human animals, and these variables can be controlled. Second, the ability to estimate θ is greatly improved when members of the same homogeneous forces are pitted against one another in different starting ratios (e.g. 80 versus 20 and 20 versus 80). Historical data on human battles rarely offers this kind of comparison in circumstances that are otherwise constant. Third, θ can be estimated more precisely if mortality rates are high. In modern human battles, mortality rates are typically much lower than for the ant battles reported here. For example, the mean mortality rate during human battles that took place from 1861 to 1982 ranged from 0.2 to 15% per day (Dupuy 1987), compared to the mean casualty rate of 42% for battles among *S. invicta* (table 1).

The values of θ vary for different size combinations even within a colony pair (table 2). There is substantial variability in the value of θ between different colony pairs, as illustrated by the lack of overlap between some 95% credibility intervals (table 2). These differences may be due to the age, past experiences, or recognition abilities of different groups of ants.

The estimated relative individual fighting abilities R showed no clear pattern. Although larger fire ant workers are usually more effective at fighting (Morrison 2000), this was not always true in this study. An inability to recognize enemies, or variability in the propensity of individuals to fight may sometimes result in larger individuals failing to attack non-nestmates, lowering their realized fighting ability.

Franks & Partridge (1993) suggest that a colony would benefit more by generating large numbers of smaller individuals than fewer large ones if group battles are common. Our results indicate that battles do not favour the size of the worker force over individual worker fighting ability to the degree hypothesized by the square law. Since it is less costly to produce small workers (Tschinkel 1988), the relative abundance of large workers suggests that the benefits of producing them outweigh the costs. Resource allocation is under strong selection (Oster & Wilson 1978), but battles do not necessarily produce the major selective force acting on the trade-off between numbers and worker size.

We expect ant species differing in worker caste compositions, weaponry, and tactics to have different values of θ ; however, values as high as 2 may be unlikely (Adams & Mesterton-Gibbons 2003). Like other ants in the subfamily Myrmicinae, workers of *S. invicta* fight with

stings and mandibles, requiring close contact in combat. By contrast, ants in the subfamily Formicinae possess acidopores which spray chemicals to damage or immobilize opponents. These differences in the methods of fighting, as well as other behavioural differences affecting the ability to concentrate attacks, are likely to affect the value of θ . Comparative studies of the relationship between fighting tactics and attrition patterns will be an interesting area for future studies.

The attrition model for which θ has been estimated (equation (2.1)) is a simplified description of battle dynamics, assuming for example that all members of a group have an identical ability and propensity to fight. Significant variation in casualty rates may occur according to the context of battle (territory or temporary food source), the mix of worker sizes and subcastes that constitute the group, and whether the fight is intra- or interspecific. Furthermore, the modified Lanchester equations quantify only one aspect of battle dynamics: the rate of attrition due to casualties. Absent from this model are parameters describing reinforcement, ability to flee, and assessment. This simplified model matches the circumstances of the experiments in that fighting was highly escalated and recruitment and withdrawal were not possible, allowing a focus on mortality rates. More complete and realistic mathematical models of aggressive interactions could improve understanding of community dynamics and territory maintenance, and provide insight as to the convergent evolution of castes and territoriality in social insect taxa.

We thank W. Tschinkel for advice and use of facilities at Florida State University, and ARVIDA for access to their property. This work was supported by National Science Foundation grant IBN-9874451 to E.A.

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