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Territory area and colony size in the fire ant *Solenopsis invicta*

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Summary

1. The allometry of colony mass to territory area governs the total biomass of ants that a given habitat supports. This relationship serves as an important link between the performance of individual colonies and the behaviour of populations experiencing density-dependent competition for space.

2. Territory area, colony mass, and the numbers of ants of each caste and developmental stage, were measured for colonies of the fire ant *Solenopsis invicta* across a wide range of sizes.

3. Most of the variation in territory area was explained by colony size, measured either by worker number, worker biomass or colony biomass.

4. The nature of this relationship was linear in May, when colonies were near their annual minimum size, but non-linear in November, when they were near their annual maximum. Territories of a given size were occupied by larger colonies in November than May, probably because in this saturated population the simultaneous increase in worker number in all colonies occurred without room for territorial expansion.

5. Mound volume, which can be quickly measured without disturbing the colony, provided a reasonable estimate of colony or worker biomass and explained most of the variance in territory size.

Key-words: competition, ecology, foraging area, population biology, seasonality.

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Introduction

Among sessile organisms that compete for space, the allometry of individual mass to area over which resources are taken has important consequences for population dynamics. This aspect of population ecology has been discussed best in the literature on plants, in which numerous studies explore the effects of mass/area relationships upon 'self-thinning' curves, the accumulation of biomass, and the development of variation and skewness of size distributions in cohorts of competing plants (e.g. Yoda *et al.* 1963; White 1981; Westoby 1984; Weller 1987). A smaller number of studies on benthic marine invertebrates (Wethy 1983; Hughes & Griffiths 1988), social insect colonies (Adams & Levings 1987) and mobile, solitary insects (Begon, Firbank & Wall 1986) has also emphasized the role of size allometries in population regulation.

In each of these groups, there may be considerable variation in size, with larger individuals taking contested resources over a greater area than small individuals. If the relationship between mass and area is isometric, and if available space is filled, then the total mass of the population is constant regardless of the sizes of the constituent members. On the other hand, if mass shows a non-linear scaling to area, then populations composed predominately of large individuals will show different collective properties than populations composed predominately of small individuals. For example, if mass is related to area by a power function:

$$\text{area} = a\,(\text{mass})^{b}$$

where $b < 1$, then the total mass of individuals that saturate a habitat of given area is greater for a small number of large individuals than for a large number of small ones. Similar arguments can be made for any property that is not scaled isometrically to area. Understanding these allometries is thus central in link-

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ing performance of individuals to behaviour of populations on a larger scale.

Within populations of ants, larger colonies may benefit from economies of scale, as do larger individuals of solitary species (Peters 1983). In the fire ant *Solenopsis invicta* Buren, this allows a reduction in the per gram cost of maintenance as colonies grow (Tschinkel 1993). This could conceivably allow large colonies to support more biomass per unit area than small colonies. Tschinkel (1993) has identified several other colony attributes that grow allometrically to colony size, suggesting that larger colonies may differ from small ones in ways that affect their resource exploitation and competition.

However, the relationship between colony size and territory area is unknown for all but a few species. A number of studies on uncensused colonies supported the generality that when colony size was estimated from associated traits, larger colonies held larger territories (Elton 1932; Pontin 1961; Wilson, Dillier & Markin 1971; Banerjee 1975; Mabelis 1979). Adams & Levings (1987) used total carton-nest volume of two species of mangrove termites to estimate colony biomass and showed that log territory area was isometrically related to the log total nest volume (i.e. slope = 1·0). Brian *et al.* (1967) and Brian & Elmes (1974) carried out territory and colony census estimates of *Tetramorium caespitum* over several years. They reported a modest correlation of territory area and colony biomass in most years. Adams & Levings (1987) reanalysed and log-transformed Brian & Elmes' (1974) data and found the slope not to differ significantly from 1·0. Wilson *et al.* (1971) estimated territory area for censused fire ant colonies, but their sample was too small to allow estimation of regression parameters.

Much of the literature on territory in social insect colonies has focused on the types of territory, their economic aspects and the behaviours involved in their defence (Hölldobler & Lumsden 1980). Aggression between neighbours, occasionally including full-scale wars, has been commonly identified as the mechanism through which colonies gain and defend territory [Brian *et al.* 1965 (review); Wilson 1971 (review); Wilson *et al.* 1971; Carroll & Janzen 1973 (review); Rockwood 1973; Hölldobler 1979; Mabelis 1979; Levings & Adams 1984; Adams & Levings 1987]. Regular spacing of colonies is considered to be a common result of such intercolony aggression, but defence of potential foraging ground (territory) is only one of several types of resource defence in ants (Eisenberg 1972; Levings & Traniello 1981; Savolainen & Vepsalainen 1988). Many species of ants compete both intra- and interspecifically, leading to mosaics of distribution (Greenslade 1971; Leston 1973; Majer 1976). Hierarchically varying competitive ability and its effect on exclusion and coexistence has been invoked as an organizing principle of ant communities (Savolainen & Vepsalainen 1988).

The details of territorial acquisition and defence are sketchy. Adams (1990) showed that the colony with the greater local density was likely to prevail in boundary disputes, and that colonies weakened by removal of a portion of their worker force lost territory to their neighbours. Mabelis (1979) indicated that the colony recruiting more warriors to battle was likely to make territorial gains. Hölldobler & Lumsden (1980) incorporated cost–benefit reasoning into economic models of territorial defence in ants. Franks & Partridge (1993) provided a theoretical framework with respect to battle strategies adopted by ants in interspecific struggles.

The nature of the limits to population growth in territorial social insects is not well understood. Because colonies can vary enormously in size, there is no single limiting density of colonies, nor is there necessarily a single limiting biomass density (Adams & Levings 1987). In this paper, we report the relationship between the size of censused colonies of the fire ant *Solenopsis invicta* and the area of territory they defend, providing a link between the performance of individual colonies and population-level measures.

Materials and methods

The study site was a 16-ha pasture about 8 km east of Tallahassee, Florida, USA. The pasture had never been subjected to fire ant control, although cattle grazed it at intervals. The population of fire ants in the pasture had therefore been undisturbed since fire ants first appeared in the Tallahassee area about 30 years previously. Although the majority of the colonies were large and mature, all stages of recruitment were also present, as expected in a stable population.

Colonies were sampled in June 1991 ($n = 24$), May 1992 ($n = 16$) and November 1992 ($n = 15$). In 1991 only mound volume and territory area were determined, but in 1992 a full colony census was also taken on the two sets of colonies. Colonies for sampling were chosen to represent the full range of colony sizes. Size was estimated from mound volumes calculated from mound dimensions. Efforts were made to weight representation towards very small and very large colonies in order to increase the power of the regressions, but normal-score analysis showed that neither the May 1992 nor the November 1992 sample deviated significantly from normality. The combined sample, however, was significantly non-normal, primarily as a result of over-representation of small colonies.

Territory area of each colony was determined by testing for hostility between workers from neighbouring colonies (Brian, Hibble & Stradling 1965; Hölldobler 1979; Adams & Levings 1987). Small test tubes containing bits of canned tuna fish were laid at 1-m intervals along 8 radii centred on the focal colony, spaced approximately every 45° like the spokes of a wheel. Canned tuna was also placed on a small piece of plywood directly on the focal mound. After about

15 min or more, most of the baits, both in test tubes and on the mound, had attracted sufficient foragers for testing. The test tubes were then carried one at a time back to the bait on the mound and, by careful manipulation of the tubes, ants from the mound bait could be induced to enter the tubes. The occurrence of aggression (biting, stinging, grappling) between tube ants and the mound ants indicated that these came from different colonies. The outermost tubes containing focal colony workers and the innermost tubes containing workers from a neighbouring colony bracketed the boundary between the colonies. By adding bait tubes between these initial limits, it was possible to pin-point most inner–outer boundaries within 20–60 cm along each baited radius. The compass angle and distance of these inner and outer limits were recorded. The territory was considered to be the area circumscribed by connecting the inner territory limit points on adjacent radii.

After the measurement of territory size, the colonies were censused as in Tschinkel (1993). The colony was excavated into a bin, the dirt and ants were homogeneously mixed, and the total soil and ants weighed. From this mixture, four samples of 150 g were randomly composed from small increments and returned to the laboratory. If sexuals were present, four additional samples of 800 g each were taken solely for determining sexual counts. If the excavated nest soil exceeded the bin capacity, a 1- or 2-kg sample from each 50 lb was reserved for final mixing and sampling. Whereas this method is reliable for estimating the excavated ants, it does not estimate the foragers afield at the time of excavation (see Tschinkel 1993 for details).

All adults (workers; male and female alates) and brood stages (worker larvae and pupae; sexual larvae; male and female alate pupae) were separated and counted in the laboratory. When these counts were multiplied by a factor obtained by dividing the total soil weight by the sample weight (150 g), an estimate of the total population of that stage or type was obtained. The mean of four such estimates was used as the base datum for this study.

A sample of each stage and caste of ant was oven-dried for dry weight determination. The product of the mean dry weight of each stage and type and its estimated population gave the biomass of that type or stage. The sum of the biomass of all stages and types gave the total colony biomass.

This procedure was applied to 16 colonies in May 1992, when colonies were near their annual minimum size (Tschinkel 1988), and 15 more in November 1992, when they were near their annual maximum.

Territory areas were regressed against three measures of colony size (number of workers, worker biomass, colony biomass), using dummy variables for the sample date (May or November). All data were log-transformed to equalize the variance, and the statistical assumptions were checked by analysis of residuals. A single outlier whose standardized residual exceeded 3·0 in all analyses was eliminated. The results of these regressions can be found in Table 1.

Results

Territory area increased strongly with colony biomass (both log-transformed), such that variation in biomass explained most of the variation in territory area. However, this relationship was different in May 1992 and November 1992 (Table 1, regression 1; Fig. 1). In May, the slope of the regression was 0·98 and was not significantly different from 1·0 (*t*-test). In November, the slope was 0·62, significantly lower than that in May (Table 1, regression 1). Therefore, a 10-fold increase in colony biomass resulted in a 10-fold increase in territory in May, but only a 4·2-fold increase (i.e. anti-log 0·62) in November. The intercept was larger in November than in May because the two regression lines crossed at 7700 mg. As a result, above about 7700 mg, colonies of a given size held larger territories in May than November. Alternatively, territories of a given size were occupied by larger colonies in November than May. Below 7700 mg of colony biomass, the reverse was true, but even at the intercepts these differences were not quite significant ($t = 1·83$, df = 24).

Territory area increased in a similar fashion with worker biomass (both log-transformed; Table 1, regression 2). Eighty per cent of the variation in territory area was explained by variation in worker biomass. The slope in May was not significantly different from 1·0 (slope = 1·07; $t = 0·36$; df = 25; NS), while that in November was significantly smaller than 1·0 (slope = 0·60; $t = 2·74$; df = 25; $P < 0·02$). A 10-fold increase in worker biomass in May resulted in a 10-fold increase in territory area, while in November it yielded only a 4·1-fold increase. As with colony biomass, worker biomass also indicated that territories of a given size were occupied by larger colonies in November than in May. Once again, the regression lines crossed, so that the reverse was true for small colonies (<2300 mg), as indicated by the significantly smaller intercept for May than November (Table 1, regression 2).

When the territory area was regressed against the number of workers (both log-transformed; Table 1, regression 3, Fig. 2), the slope was larger than 1·0 in May but not quite significantly so (slope = 1·31; $t = 1·55$; df = 25; NS). In November, the slope was less than 1·0 and significantly smaller than the May slope (slope = 0·77; Table 1, regression 3). Thus, in May a 10-fold increase in the number of workers resulted in a 20-fold increase in territory, while in November it resulted in only a 5·9-fold increase. As above, the November intercept was higher than that in May, although not quite significantly so (Table 1, regression 3). Above a minimum colony size (7700

Table 1. Regressions of the variables of this study. All variables were log-transformed before regression. Sample month was entered as a dummy variable. The *P*-values refer to differences between coefficients for sample months. Coefficients not significantly different from 0·0 are shown in bold. Sample size in both May and November = 15

				Slope (a)		*y*-intercept (b)		
Regression number	*y*-variable (log)	*x*-variable (log)	Sample month	Coefficient	*P*	Coefficient	*P*	R^2 (%)
1	Territory area	Colony biomass	May 1992	0·98	NS	−2·74	0·05	79
			November 1992	0·62		−1·34		
2	Territory area	Worker biomass	May 1992	1·05	0·02	−2·76	0·05	80
			November 1992	0·61		−1·28		
3	Territory area	Worker number	May 1992	1·29	0·05	−4·34	NS	76
			November 1992	0·77		−2·29		
4	Biomass density	Colony biomass	May 1992	**0·02**	0·05	2·74	NS	40
			November 1992	0·38		1·34		
5	Worker density	Worker number	May 1992	**−0·31**	0·05	4·39	NS	
			November 1992	**0·23**		2·29		
6	Mound volume	Colony biomass	May 1992	1·30	NS	4·81	NS	90
			November 1992	1·28		4·48		
7	Territory area	Mound volume	May 1992	0·89	0·001	0·69	0·001	92
			November 1992	0·50		1·14		
8	Territory area	Mound volume	June 1991	0·67		1·09		82
9	*x* weight workers	Number of workers	May 1992	0·20	NS	−1·39	NS	42
			November 1992	0·28		−1·78		

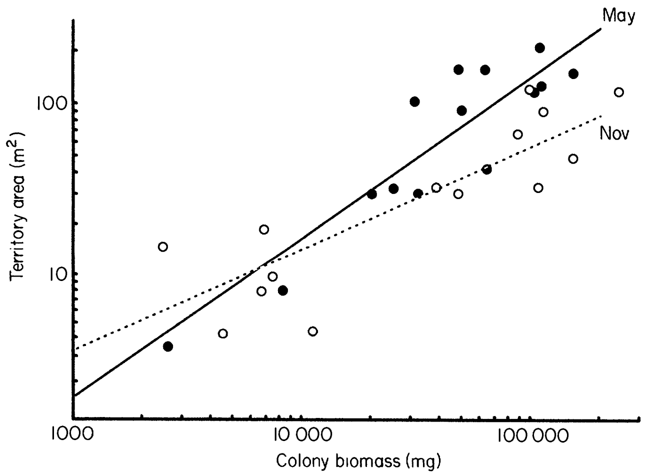

Fig. 1. The relationship between territory area and colony biomass (log scales). The slope of the regression was higher in May (closed circles) than November (open circles) 1992. Territories of a given size were occupied by larger colonies in November than in May.

Fig. 2. Relationship between territory area and the number of workers (log scales). Territories of a given size contained more workers in November (open circles) than May (closed circles) 1992.

workers), territories of a given size were occupied by larger colonies in November than in May.

The higher regression slopes for worker number than for worker biomass were the result of the increase in mean weight of workers as colony size (number of workers) increased (Tschinkel 1993; Table 1, regression 9). Therefore territory increased less rapidly in relation to worker biomass than to worker number in both samples.

These regression slopes indicated that in May the biomass of colony or workers supported per m^2 was unrelated to colony or territory size, while in November larger territories supported a higher biomass per m^2. This was confirmed by regressing colony biomass per m^2 against colony biomass (both log-transformed). The slope of this regression was not significantly different from 0 in May, but was positive in November (Table 1, regression 4).

For worker density, the best estimate indicated that the number of workers per m^2 decreased with colony size in May (slope = 0·31) but increased in November (slope = 0·23). These slopes differed significantly from one another (Table 1, regression 5), but neither was significantly different from zero. Averaged over the total colony population, the area defended per worker increased with colony size in May, but decreased in November.

Perhaps the most convenient estimate of colony size is mound volume. Tschinkel (1993) found that 85% of mound volume variation was explained by variation in colony biomass. In this study, a 10-fold increase in colony biomass resulted in a 20-fold increase in mound volume. The relationship was not significantly different for May and November (Table 1, regression 6). The strength of this relationship suggested that mound volume might serve as an estimate for colony biomass. The relationship between mound volume and territory was estimated in the spring of 1991 and twice in 1992 (Table 1, regressions 7 and 8; Fig. 3). The slope of the June–July 1991 sample was intermediate between the slopes of the May and November samples of 1992, but it was not possible to assign these differences to interannual variation, seasonal variation or chance. A 10-fold increase in mound volume in May resulted in a 7·8-fold increase in territory area, while in November it resulted in only a 3·2-fold increase. The May factor was 2·4 times larger than the November one, just as it was for the relationship of territory to biomass, and as expected if mound volume grew at the same rate as colony biomass. A colony with a one litre mound occupied 4·9 m^2 in May, but a colony of this size held only 1·7 m^2, or 35% as much, in November. Variation in mound volume explained 92% of the variation in territory size.

Discussion

Colony size, in its various manifestations, was a strong predictor of territory area (and perhaps vice versa), accounting for 75–80% of the variance. Territory area increased with the size of the colony, but did so at about half the rate in November as in May. Territories of a given size were occupied by larger colonies and a greater biomass of ants per m^2 in November than in May.

These patterns can be interpreted in light of known seasonal and life-history changes. The worker population of colonies declines from mid-winter to mid-summer while sexuals are being produced, and increases during the second half of the year after sexual production has ceased (Tschinkel 1993). The worker population of colonies therefore varies up to almost twofold between these seasonal extremes, and the degree of variation is proportional to colony size. May colonies are close to their annual minimum, while November colonies are near their annual maximum.

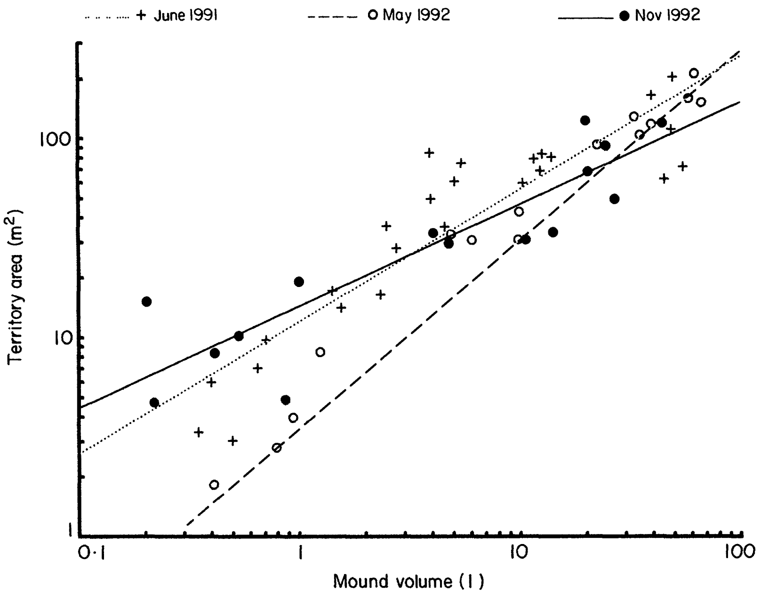

Fig. 3. Relationship between territory area and mound volume (log scales). Mound volume could be used as an adequate estimate for colony biomass, because variation in colony biomass explained 90% of the variation in mound volume. Data for June–July 1991 are included along with the May and November 1992 data.

In spite of these dramatic increases in colony size from May to November, there are only limited opportunities for territorial expansion because territories fill the area even when colony size is at its seasonal minimum (the density of mature colonies varied little over the year (E.S. Adams & W.R. Tschinkel, unpublished data). As colonies grow towards their seasonal maximum, large colonies gain biomass at a greater rate than small colonies (Tschinkel 1993), yet this study showed that the increase in biomass was not matched by proportional gains in territory area. As a result, territory area in November did not increase linearly with colony mass (Fig. 1). While the underlying behavioural cause is not known, it may be that territory boundaries are slow to change in relation to biomass due to 'inertia' in the behaviour of ants at previously established borders, or that the territory-holding ability of the colony rises less rapidly than the number of workers. This suggests that colonies undergo their annual size fluctuation within relative fixed territories. They may make net annual gains, but probably show little cyclic territorial variation in a fully packed site. In this circumstance, territory can be gained primarily at the expense of the territory of neighbours, either through net colony growth, or the demise or attrition of neighbours.

Because colony density changed little across the period of study (E.S. Adams & W.R. Tschinkel, unpublished data), these results point to dramatic seasonal fluctuations in the total number and biomass of ants supported within the study habitat. The non-linear relationships documented here show that aggregate features of the ant populations depend in complex ways upon the size distribution of colonies. In May, territory area was scaled linearly to colony biomass, implying that large and small colonies supported roughly the same biomass per unit area. However, in November, when the ant population was close to its peak level, larger colonies supported a greater biomass of ants per unit area than did small colonies. Thus, the total number of workers, the production of alate sexuals, patterns of energy flow through the *S. invicta* populations, and potentially the impact of the ants on other species, will vary with the size distribution of ant colonies. These properties are likely to change as the population of colonies ages until an equilibrium distribution is reached.

Although territory is gained and defended through the aggressive behaviour of workers (Wilson 1971; Hölldobler 1979; Hölldobler & Lumsden 1980; Adams 1990), little is known about territorial behaviour in fire ants. Wilson *et al.* (1971) reported fights at territorial boundaries, but the quantitative relation between worker number and the outcome of interactions is not known. In *Azteca*, workers recruit nestmates for defence, and outnumbered groups of workers tend to withdraw from the field of battle to easily defended points in their arboreal territories (Adams 1990). Mabelis (1979) noted that colonies of *Formica polytena* that fielded more warriors were more likely to gain territory, while Hölldobler (1981) reported that *Myrmecocystus mimicus* colonies overrun colonies having a much smaller worker force. The theoretical contributions of Franks & Partridge (1993) to interspecific ant battles might, with modification, also illuminate intraspecific battles. Several of these studies suggest that asymmetries in worker number or in worker size affect the outcome of competitive struggles; however, the quantitative relationship between the strength of the asymmetry and the amount of territory gained has not yet been documented for any ant species.

Fire ants defend a continuous perimeter and one might expect territorial success to be strongly related to how much colonies allocate to the perimeter force. However, it must be remembered that neighbours also allocate resources to their perimeter defence. The actual outcome must therefore be the result of some combination of relative allocation and behaviours such as speed and effectiveness of recruitment, the size and defence allocation of other neighbours, and other factors.

The proportion of the worker force that fire ant colonies allocate to perimeter defence is not known. Presumably, this defensive force is drawn from the forager population. In laboratory colonies, the proportion of the worker force that foraged declined with colony size (Mirenda & Vinson 1981), but this relationship is not known for field colonies. Geometrically, however, the perimeter grows in proportion to the territory radius, while foraging area grows in proportion to the square of this radius. Thus, as colonies grow, they could conceivably maintain the same density of defensive force at the perimeter of their expanding territory, while allocating a declining proportion of their forager and worker force to defence. This suggests that the cost–benefit ratio of territorial defence might become increasingly favourable as territory size increases. In addition, colonies could defend the same perimeter with a smaller proportion of their worker population in November than in May because the worker force increases more than the perimeter. The November worker population is also younger (Tschinkel 1993) than the May one, adding credence to the hypothesis that a smaller proportion defends and forages in November. Knowledge of the allometries among colony size, territory size, the proportion of foragers and the proportion of defenders would undoubtedly illuminate the colony's territorial strategy. Coupled with the allometries among colony size, sexual production, worker maintenance and replacement costs (Tschinkel 1993), it may be possible to link individual colony fitness with territory size.

The complexity of these potential interactions may explain, in part, why colonies of the same biomass may differ by almost threefold in territory area (±1 SD; Fig. 1). In addition to variation caused by environmental heterogeneity, the actual territory size may be the outcome of the interaction among the colony's own size and defence capability and that of its neighbours, individually and aggregated. A colony may hold less territory when surrounded by larger neighbours or more neighbours. We are developing neighbourhood models of fire ant territories to be published elsewhere (E.S. Adams & W.R. Tschinkel, manuscript in preparation).

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