Mechanisms of population regulation in the fire ant *Solenopsis invicta*: an experimental study

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Summary

1. We tested for density-dependent regulation of biomass in a population of the fire ant *Solenopsis invicta* and examined the mechanisms of population recovery following replicated colony removals.

2. All colonies were killed within the core area (1018 m²) of six plots, while six additional plots served as undisturbed controls. Over the next 5 years, colonies were mapped several times per year and the biomass of each colony was estimated from the volume of the nest-mound.

3. The average biomass and density of colonies within the removal areas gradually converged on those of control plots and were no longer detectably different after two years. Thereafter, ant biomass on experimental and control plots showed nearly identical seasonal and yearly fluctuations.

4. Territories of colonies surrounding the removal areas rapidly expanded following the deaths of neighbours, while average territory size on control plots showed little short-term change.

5. Significantly more new colonies were established within core areas of experimental plots than within core areas of control plots during the first year following removals.

6. The per-colony probability of movement and the net influx of colony biomass were significantly higher in central regions of the experimental plots than in control plots during the first year. The directions of colony movements were clustered towards the centres of experimental plots in the first 2 years, but did not show significant directional trends on control plots.

7. In all 5 years of the study, annual mortality rates were lower for larger colonies, but the size-specific risk of mortality was not significantly affected by the experimental removal of competitors.

8. The growth rates of colonies, adjusted for initial size, were significantly higher in central regions of experimental plots than in control plots during the first two years of the study. In all years, colony growth rates declined with increasing colony size.

9. These results indicate that populations of *S. invicta* are regulated by competition among neighbouring colonies. Due to large intraspecific variation in colony size, the dynamics of ant populations are described more accurately by measures of total ant biomass than by colony density alone.

Key-words: convergence experiment, density dependence, population dynamics, social insects, territory size.

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Introduction

The nature of population regulation is the subject of long-lasting debates among ecologists. While much ecological theory assumes that populations are regulated by density-dependent processes, there is continuing scepticism as to whether this assumption is upheld by data (e.g. Strong 1986; Wolda 1989; den Boer & Reddingius 1996). This disagreement arises in part because fluctuations in density can be caused either by density-independent processes, or by density

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dependent processes pushing populations to levels that change with environmental conditions. In addition, density-dependence can be either 'noise-reducing', tending to dampen changes caused by external perturbations, or 'noise-amplifying', producing chaotic dynamics (Ellner & Turchin 1995). These alternatives can be difficult to distinguish by analyses of time series alone, especially when densities are measured with error (Gaston & Lawton 1987; Wolda & Dennis 1993; Shenk, White & Burnham 1998).

Ecologists have long recognized that controlled field experiments can detect the presence of density-dependent processes. An important approach, known as a convergence experiment (Murdoch 1970), was described as early as Nicholson's (1957) discussion of population regulation. In a convergence experiment, the tendency of populations to return to an equilibrium is evaluated by experimentally altering densities in one or more subpopulations, and then monitoring the subsequent dynamics of these subpopulations relative to controls. If the population is regulated by nonchaotic density-dependent processes, then densities at perturbed sites will converge on those of controls, even when the equilibrium density fluctuates due to environmental variation (Murdoch 1970). Convergence of densities at perturbed and control sites indicates that density-dependence is noise-reducing, or characterized by a negative Lyapunov exponent (Ellner & Turchin 1995; Turchin 1995).

Despite the power of this experimental approach, it can be difficult and time-consuming and is not often implemented (Sinclair 1989). Experimental manipulations of animal densities are often restricted to part of the life cycle or to small spatial scales (Harrison & Cappuccino 1995). None the less, enough information has accumulated from statistical and experimental analyses to allow comparative approaches to the study of population dynamics (e.g. Cappuccino & Price 1995). To date, reviews of studies on insect population dynamics are based almost entirely on non-social species (e.g. Stiling 1988; Hassell, Latto & May 1989; Sinclair 1989; Turchin 1990). Much less is known about the population dynamics of social insects, even though they are abundant and ecologically important in many terrestrial habitats. Although studies on ant populations continue to accumulate (e.g. Pontin 1961; Brian, Elmes & Kelly 1967; Brian & Elmes 1974; Mabelis 1979; Davidson 1985; Fowler *et al.* 1986; Ryti & Case 1988; Adams & Tschinkel 1995a; Wiernasz & Cole 1995; Gordon & Kulig 1998), long-term records of social insects populations are relatively uncommon. Contributing causes include the comparatively long generation times of social insect colonies, and a historical emphasis by social insect ecologists on behaviour (Bourke & Franks 1995; Crozier & Pamilo 1996) or community interactions (e.g. Huxley & Cutler 1991), rather than on the population dynamics of particular species. An additional reason is that, while it is often easy to locate ant colonies, it is usually difficult to estimate the sizes of

colonies, especially for species with subterranean nests. Due to substantial intraspecific variation in worker population across colonies, fluctuations in colony size may contribute as much or more to changes in insect biomass as fluctuations in colony number.

A large body of evidence indicates the importance of intra- and interspecific competition in controlling ant populations, with effects on colony establishment (e.g. Hölldobler 1976; Majer 1976; Davidson 1985; Chew 1987; Fowler 1987; Ryti & Case 1988; Gordon & Kulig 1996; Jerome, McInnes & Adams 1998), movement (de Vita 1979), mortality (Adams & Tschinkel 1995a; Gordon & Kulig 1998), size (Ryti & Case 1986), reproductive output (Pontin 1961; Gordon & Wagner 1997), and the spatial pattern of nests (e.g. Elmes 1974; Traniello & Levings 1986). However, much of the evidence concerning the effects of intraspecific competition is based on correlations rather than experiments. In addition, it is rare for all of these components to be followed in the same study; thus, little is known about their relative importance or about the quantitative nature of the population dynamics that they produce. As a consequence, models of social insect population dynamics (e.g. Ryti & Case 1992; Korzukhin & Porter 1994; Stoker *et al.* 1994) lag far behind those of solitary insects or other well-studied taxa and none are well tested.

This study tested experimentally for density-dependent population regulation in populations of the fire ant *Solenopsis invicta* (Buren) in pasture in north Florida, in the south-eastern United States. *S. invicta* is native to South America and has become an important and widespread pest following its accidental introduction to the United States (Lofgren 1986). In a replicated field experiment, colonies were removed from central areas of six experimental plots. We followed changes in colony size, position and number in these plots and on six undisturbed control plots over the next 5 years. In total, the study included more than 1000 colonies in an area greater than 4 ha. In addition to testing for density-dependent regulation of ant biomass at the level of the population, we examined the effects of ant density on four potential components of population recovery: the establishment of new colonies, colony movement, colony mortality, and colony growth. We also examined the responses of territory size to the removal of neighbours.

Methods

STUDY SPECIES

The history of *Solenopsis invicta* (Buren) in the United States has been reviewed by Lofgren (1986) and its reproductive biology by Tschinkel (1998). Colonies of *S. invicta* construct above-ground nest-mounds and live within these mounds and in chambers extending beneath them (Markin, Dillier & Collins 1973). Two social forms are known: a monogyne form, with a single egg-laying queen in each mature colony, and a

polygyne form, which often has multiple egg-laying queens per nest (Tschinkel 1998). Whereas colonies of the monogyne form are territorial, ants from different nests of the polygyne form intermingle without aggression and populations consist of interconnected nests that reproduce by budding (Vander Meer, Obin & Morel 1990). Because of differences in social structure, these two forms undoubtedly have very different patterns of population dynamics. At our study site in Leon County, Florida, only the monogyne form has been found (Porter 1992; personal observations). Monogyne social structure at this site was confirmed by the size of the largest workers (Porter 1992), by the defence of territories (see below; Tschinkel, Adams & Macom 1995), by nest excavations (Tschinkel 1993; Tschinkel 1996), by the low production of diploid males and by colony genetic structure (de Heer & Tschinkel 1998), and by the comparatively low colony density and large nest size (Macom & Porter 1996).

STUDY SITE

Twelve circular study plots, each 72 m in diameter, were established in pasture near Tallahassee, Florida, in the spring of 1991. For a more complete description of the study site, see Tschinkel *et al*. (1995). The plots were scattered over an area approximately 300×600 m in areas lacking mature trees or other tall vegetation. The centre of each plot was marked by a 30×30-cm metal plate held in place by bolts inserted deep into the soil.

FIELD METHODS

Several times per year, each plot was surveyed and the positions and sizes of active nests were recorded. Two to four people thoroughly searched each plot by walking through it in closely spaced parallel lines. All but the smallest nests (those less than 0·5 L) are easily located by visual inspection. Occupied nests were identified by repeatedly inserting a 40-cm wire into each nest. If the nest is occupied, this disturbance causes workers to rush out of the holes that are created. (Exceptions occurred during the late summer – see below.) The position of each occupied nest was marked with a numbered aluminium tag nailed into the soil. We used a fibreglass tape measure to determine the distance to the centre of the plot and a sighting compass to determine the direction to the nest from the centre of the plot. Because compass measurements were not sufficiently accurate at greater distances, colony positions were corrected by triangulation, using the distances between nest sites.

At each census, the size of each active nest was estimated by measuring the length, width and height of the nest-mound with a pair of tree calipers. The volume of the above-ground portion of the nest was then estimated by treating these measurements as the axes of an ellipsoid (Tschinkel 1993). The relationship between this estimate of nest volume and the biomass or
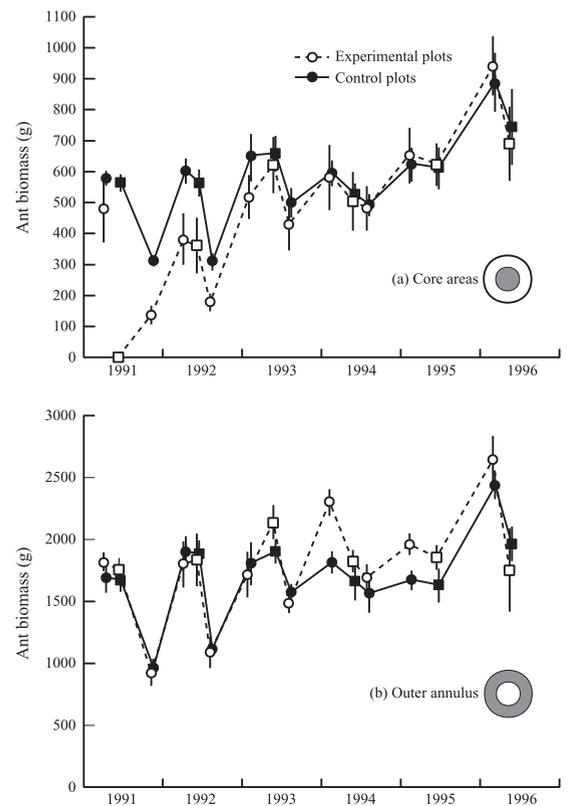
Fig. 1. Total estimated biomass of fire ants on experimental and control plots (mean ± SE) in (a) core areas (< 18 m from the plot centre), and (b) outer annuli (18–36 m from the plot centre). The area of the outer annuli was three times that of the core area. The left-most symbols indicate measurements taken prior to the experimental removals; colonies were removed from core areas of experimental plots after these measurements. Square symbols indicate censuses taken in late spring.

number of ants within the nest was previously calibrated at the same study site; however, the resulting biomass estimates omit foragers away from the nest at the time of excavation (Tschinkel *et al*. 1995).

Each year, all plots were censused in late May or early June. Additional censuses were carried out opportunistically. Censuses required at least two weeks to finish. Figures 1 and 2 show the dates at the midpoints of each census: May 8, June 10 and November 9, 1991; April 4, June 5 and August 6, 1992; February 1, May 24 and August 4, 1993; February 6, May 25 and July 28, 1994; February 9, 1995 and June 14, 1995; February 28 and May 15, 1996. In addition, the positions of all active colonies were mapped, without measuring nest-mounds, in August 1991 and in July 1996 to detect colony movements.

The history of population change was reconstructed by comparing sequential maps. Most colonies remain in the same position from one census to the next, so that comparisons in size were easily made. Newly established colonies became visible if they survived long enough to produce a nest-mound of approximately 0·5 L. Some colonies dwindled in size and
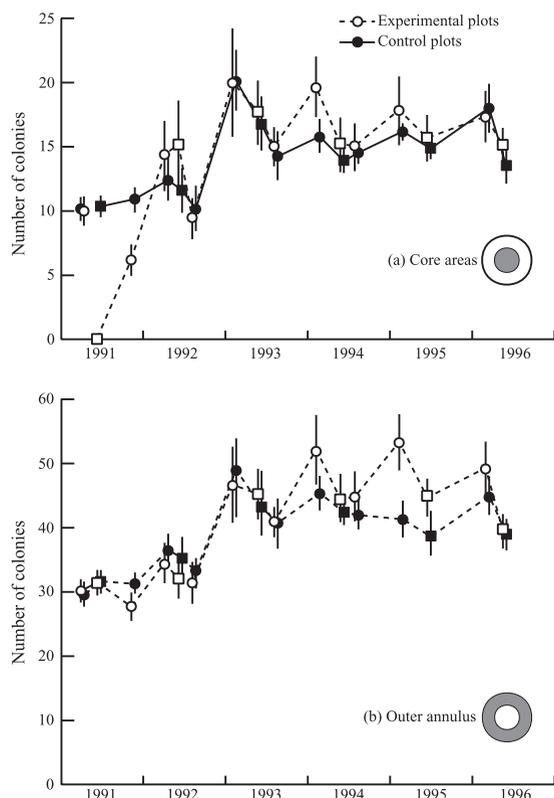
Fig. 2. Total numbers of colonies on experimental and control plots (mean ± SE) in (a) core areas and (b) outer annuli. Symbols as in Fig. 1.

became inactive, indicating colony death. In most cases, the birth or death of a colony was unambiguous. However, colonies of *S. invicta* occasionally relocate from one nest site to another (Hays *et al*. 1982; Fuller, Hays & Stanley 1984) and some colonies temporarily use more than one nest (Byron & Hays 1986). For large colonies, relocations were fairly easily deduced when a nest-mound active at one time was inactive at the next census, while a new nest-mound of approximately the same basal area appeared within a few metres. For very small colonies, it was often not possible to distinguish colony relocation from the near simultaneous death and birth of two distinct colonies that were close to one another. Because we wished tests of size-related mortality to be conservative, we scored these cases as nest relocations whenever the two nest sites were within 3–4 m, with no other colonies between the two sites. A second problem is that workers do not always respond when the nest is pierced by a wire probe in hot, dry weather, when the ants tend to remain deep underground; therefore, some active colonies were incorrectly scored as inactive. This was apparent when a large colony was active in a series of censuses, with one intervening score of apparent inactivity, and when there was no sign of migration. In these cases, we assumed that the colony was alive at the intermediate census, and estimated the biomass for that date by interpolating between measurements at the previous and subsequent censuses.

REMOVAL OF COLONIES

Each circular plot was divided into a 'core area' within 18 m of the plot centre (area = 1018 m^2), and an 'outer annulus', consisting of the region between 18 m and 36 m from the plot centre (area = 3053 m^2). In addition, many colonies beyond the 36-m radius were mapped to help determine the origins and destinations of colonies moving on or off the study plots.

Six of the 12 plots, selected randomly, served as experimental plots while the other six were undisturbed controls. In experimental plots, all detectable colonies within the core areas were killed in the spring of 1991, from mid-April to mid-June. Two methods were used. First, each colony in the core area was given several ml of Amdro (American Cyanimid, Princeton, New Jersey, USA), a pesticide carried on food baits. The toxin in Amdro breaks down quickly, leaving no detectable residue after 48 h (Apperson, Leidy & Powell 1984). Secondly, any remaining colony fragments were killed by driving a metal stake deep into the nest-mound and filling the nest chambers with boiling water.

STATISTICAL ANALYSES

Because the experimental perturbations were conducted in spring, statistical analyses were based on periods of 1 year lasting from one spring census (late May or early June) to the next. Large parts of one control plot and one experimental plot were disturbed by a tractor with a 'bush-hog' attachment for clearing brush in April 1992, during the first year of the study, with effects lasting into the second year. Since this affected the sizes of the nest-mounds and made it especially difficult to distinguish colony relocation from death, we excluded these two plots from analyses for the first 2 years, or else used censuses only up to the time of disturbance.

Statistical analyses were conducted with Systat 7·0 (SPSS Inc., Chicago, IL, USA).

TERRITORY SIZES

We tested for changes in territory size for colonies just outside the core areas during the first 2 months following the removals. For three experimental plots and three control plots, two colonies were selected that were outside the core area but whose territories abutted those of colonies within the core area. The two colonies selected on a given plot were well separated, in roughly opposite directions from the plot centre. Foraging territories for these colonies were mapped before the removals and again eight weeks later. Territories were mapped by testing for aggression between ants attracted to numerous baiting sites (see Tschinkel *et al.* 1995; Adams 1998). Preliminary statistical tests confirmed that territory sizes did not deviate significantly from normal distributions, that variances on experimental and control plots did not differ significantly, and that there were no significant plot effects.

NEW COLONY ESTABLISHMENT

New colonies are founded by queens following mating flights (Markin *et al.* 1971). The largest flights occur in late spring and early summer (Tschinkel 1993). To test whether the experimental removals led to an increased rate of new colony establishment, we counted new colonies that appeared at any census and that survived to the end of the study year.

SURVIVAL

For each year, we tested whether the probability of colony survival was affected by the initial size of the colony or the experimental removal of other colonies in the study plot. Because deaths of neighbouring colonies may not be independent events, a subset of colonies from each plot was selected, subject to the requirements that selected colonies were at least 15 m apart from one another and were within 25 m of the centre of the plot. The 25-m limit includes colonies within the core areas or that were immediate neighbours of colonies in the core areas. Among the many sets of colonies that would fit these criteria, a set was chosen with a wide range of colony sizes, including the largest and smallest on each plot when possible.

In testing whether the experimental removals significantly affected the mortality rates of surrounding colonies, it was necessary to consider whether survivorship varied with colony size. Logistic regressions were performed for each year with survival as the dependent variable (each colony either survived or did not survive until the end of the year), and the logarithm (base 10) of colony mass as the dependent variable. To assess whether this model gave a good fit to the data, the data from each analysis were divided into quintiles of roughly equal size and the goodness-of-fit of the observed proportions surviving to those predicted by the logistic regression was assessed by the Hosmer–Lemeshow statistic (Hosmer & Lemeshow 1989). Preliminary analyses for all years showed good fits to logistic regressions when colony masses were log-transformed, but not when masses were untransformed. For each year's data, we tested whether the goodness-of-fit was significantly improved by adding either treatment (experimental plot or control plot) or plot identity as categorical independent variables to the model. This was assessed by the G statistic, which is based on the logarithm of the likelihood ratio for the two versions of the model (Hosmer & Lemeshow 1989).

For illustrative purposes, an additional analysis was conducted for the fifth year of data with colonies selected as described above, but including colonies up to 36 m from the centre of the plot.

COLONY MOVEMENT

Three analyses of colony movement were conducted.

(1) Probability of colony movement

The first analysis tested whether treatment, colony size or plot affected the probability of colony movement from spring of one year until the spring of the next year. Logistic regressions were used with colony movement as the dependent variable (each colony either moved or did not move during the year of analysis), with colony mass as a continuous independent variable, and with treatment (experimental or control plots) or plot identity as dummy independent variables. Because movements of adjacent colonies may not be independent events, the colonies used in the analysis were a subset of those present, selected as described above for the analysis of survival, but with two additional restrictions. First, only colonies that survived for the entire year were used. Secondly, because of the difficulty of distinguishing small colony death from movement, colonies with initial nest-mound volumes lower than 4·0 L were excluded from the analysis.

(2) Directions of colony movement

The second analysis tested whether colonies tended to relocate towards areas from which competitors had been removed. Each colony relocation was described as a vector, with the length of the vector equal to the distance between the nest location at the start of the study year and the nest location at the end of the year. The angle of the vector was the direction from the original to the final nest site relative to a line drawn from the original nest site to the centre of the plot. Thus, a colony movement directly towards the centre of the core area had an angle of 0 degrees. Only colonies within 25 m of the centre of the plot were used, since these were most likely to be affected by the experimental removals, and only colonies with nest-mound volumes greater than 4·0 L were included. For each plot in each year, a summary vector was calculated based on the average *x*- and *y*-coordinates of the vectors for all colonies that moved. The angle of this vector was used to describe the directional tendency of colony movement for that plot. The *v*-test (Batschelet 1981) was used to test whether the angles of these summary vectors tended to cluster around 0 degrees; that is, whether colonies tended to move towards the centre of the plot.

(3) Net movement of ant biomass

The third analysis tested whether there was a net influx of ant biomass into the core areas of experimental plots; i.e. across a circle drawn 18 m from the plot centre. The net influx for each plot was calculated as the sum of the biomasses of all colonies moving from positions outside the core area to positions within the core area, minus the summed biomasses of any colonies exiting the core area. To test whether the effects of removals had detectable effects at greater distances, we also tested whether the net influx of colonies was

greater on experimental plots than on control plots across circles drawn 27 m from the centres of the plots, midway between the outside perimeters of the core area and the outer annulus.

COLONY GROWTH RATES

Colonies were selected for analysis as described above for the analysis of the probability of colony survival. Only colonies that survived and remained in place for the entire year were used. Preliminary analysis showed that the assumptions of analysis of covariance were met when colony mass at the end of the study year was the dependent variable, treatment was a fixed factor and size at the beginning of the year was the covariate. Preliminary analyses tested whether the model was improved by adding either plot (a random factor nested within treatment), interactions between mass and treatment, or both. No significant effects of these additional terms were found except in the fifth year, when there was a significant effect of the identity of the plot. Because this effect was inconsistent and occurred only in a year with no treatment effects (see below), only the simpler models are presented. Although the data fit the assumptions of the analysis of covariance, we caution that the resulting model cannot necessarily be extrapolated to very small colonies, since it would imply per-gram growth rates that are too high. For our analyses, the qualitative results were not affected by removing the smallest colonies and fits to the model assumptions were not improved by log-transformation.

Results

TERRITORY INCREASE

Territory areas of colonies in experimental plots, whose neighbours were removed, expanded an average of 45 ± 18 m^2 (mean $\pm$ SE; $n = 6$), or $122 \pm 52\%$, in 8 weeks while territories on control plots lost an average of 11 ± 15 m^2 ($n = 6$), or $7 \pm 10\%$, during the same period ($F_{1,10} = 5 \cdot 78$, $P = 0 \cdot 04$).

RECOVERY OF ANT POPULATIONS FOLLOWING COLONY REMOVALS

Figure 1a shows that, following colony removals, average biomass in the core areas of experimental plots converged asymptotically towards average biomass on control plots. Prior to the colony removals, average ant biomass in core areas of experimental plots did not differ significantly from that on control plots ($t = 1 \cdot 08$, $n = 3$ and 6, $P = 0 \cdot 32$). (Only three experimental plots were included in this analysis – the three set up last – because initial colony sizes on the other plots were not recorded prior to the removals.) Ant biomass in core areas increased significantly more on experimental plots (690 ± 120 g) than on control plots (182 ± 110 g) over the 5 years of the experiment (Mann–Whitney

$U = 2$, $n = 6$ and 6, $P = 0 \cdot 01$). At the final census, the biomass of ants on experimental plots and control plots did not differ significantly ($t = 0 \cdot 32$, $n = 6$ and 6, $P = 0 \cdot 76$). For data from the outer annuli (Fig. 1b), experimental and control plots did not differ significantly in initial biomass ($t = -0 \cdot 50$, $n = 6$ and 6, $P = 0 \cdot 63$), change in biomass over the 5-year study ($t = 0 \cdot 65$, $n = 6$ and 6, $P = 0 \cdot 53$), or in final biomass ($t = 0 \cdot 57$, $n = 6$ and 6, $P = 0 \cdot 58$).

Figure 2 shows mean colony numbers in the experimental and control plots. The number of colonies did not differ significantly between experimental and control plots before the removals were performed either in the core areas ($t = 0 \cdot 11$, $n = 6$ and 6, $P = 0 \cdot 91$) or the surrounding annuli ($t = 0 \cdot 13$, $n = 6$ and 6, $P = 0 \cdot 90$). Following the removals, experimental plots added significantly more colonies than control plots over the next 5 years in core areas ($t = 7 \cdot 74$, $n = 6$ and 6, $P < 0 \cdot 0001$), but not in the surrounding annuli ($t = 0 \cdot 14$, $n = 6$ and 6, $P = 0 \cdot 89$).

Figures 1 and 2 both show considerable fluctuations. Ant biomass fluctuated seasonally, reaching a peak in the spring before the large mating flights (Fig. 1). Some of the variation was due to changes in census dates across years. However, a census was taken in late spring each year at a standardized period, shown by square symbols on Figs 1 and 2. The consistency of the size of the population can therefore be evaluated by testing whether total ant biomass or colony density on control plots at these censuses differed significantly among years. Variances across plots were equalized by log-transformation. Repeated-measures ANOVA indicated no significant differences among years in spring ant biomass on control plots ($F_{5,20} = 1 \cdot 06$, $P = 0 \cdot 41$). However, colony densities on control plots differed significantly among years (Friedman's test statistic $= 11 \cdot 7$, d.f. $= 5$, $P = 0 \cdot 04$). Figure 2 shows that a substantial increase in colony densities occurred in 1993 on both experimental and control plots.

NEW COLONY ESTABLISHMENT

Figure 3a shows that significantly more colonies were established in core areas on the experimental plots than on control plots in the first year (Mann–Whitney $U = 2 \cdot 0$, $n = 6$ and 6, $P < 0 \cdot 001$; difference between the means $= 8 \cdot 3$), but not in later years (year 2: $U = 11 \cdot 5$; Year 3: $U = 19 \cdot 5$; year 4: $U = 19 \cdot 5$; year 5: $U = 23 \cdot 5$; $P > 0 \cdot 35$ in all cases). No differences were found between experimental and control plots in numbers of new colonies appearing in the surrounding annuli in any year (Fig. 3b; year 1: $U = 15 \cdot 5$; year 2: $U = 10 \cdot 5$; year 3: $U = 16 \cdot 0$; year 4: $U = 12 \cdot 5$; year 5: $U = 23 \cdot 5$; $P > 0 \cdot 35$ in all cases).

We tested for variation in the rate of new colony establishment across years using data from 18 to 36 m from the plot centres for both control and experimental plots, since the numbers of new colonies established did not differ between control and experimental plots
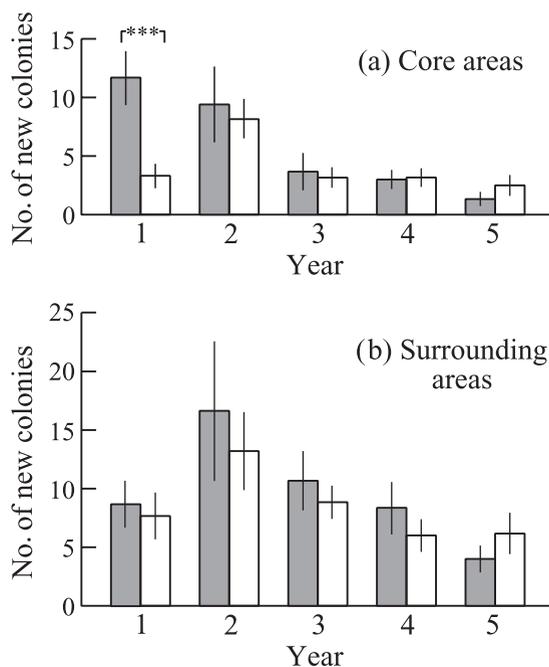
Fig. 3. Numbers of newly established colonies surviving to the end of each year of the study (mean ± SE). Shaded bars: experimental plots; unshaded bars: control plots. There was only one significant contrast between control and experimental plots (***$P < 0.001$; see text).

Fig. 4. Probability of colony survival on control plots during the fifth year as a function of initial colony size. The sample size for each proportion is shown above the bar. The solid line shows the logistic regression fitted to these data. These estimates of mortality rates are conservative, especially for small colonies.

in these regions (Fig. 3b). The number of new colonies varied significantly among years and was highest in the second year (Friedman test statistic = 12·3, d.f. = 5, $P = 0.015$).
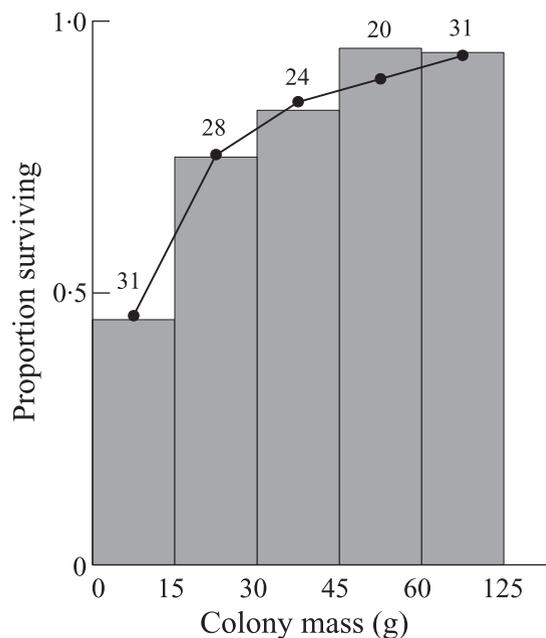
SURVIVAL

The annual probability of survival increased with colony size in each year of the study (Table 1; Fig. 4). Logistic regressions of the probability of survival against the logarithm of colony biomass provided good fits to the data (Fig. 4; Table 1; small *P*-values for the Hosmer–Lemeshow goodness-of-fit statistic would indicate lack of fit). The models were not significantly improved by inclusion of either treatment (experimental or control plots) or plot as independent variables (Table 1); thus, there was no evidence that the size-specific annual rate of mortality was affected by experimental removal of competitors.

COLONY MOVEMENT

(1) Probability of colony movement

Results of log-likelihood analysis of the probability of colony movement are shown in Table 2. Neither plot identity nor colony mass had significant effects on the probability of colony movement. In the first year following the experimental removals, colonies on experimental plots were significantly more likely to move than those on control plots (experimental: 51·7%,

$n = 29$ colonies; control: 25·8%, $n = 31$). No effect of treatment was found for any subsequent year. The percentage of colonies that moved, among those meeting the criteria for inclusion in the analysis (see methods), was 36·4% in the second year ($n = 55$), 28·6% in the third year ($n = 70$), 44·9% in the fourth year ($n = 69$), and 28·4% in the fifth year ($n = 74$). To test whether the probability of colony movement varied among years, only data from the control plots were used. The probability of movement did not vary significantly among years ($G = 6·81$, d.f. = 4, $P = 0·15$, NS).

(2) Directions of colony movement

Figure 5 summarizes the directional tendencies of colony movements. For both experimental and control plots, for each year, a vector is shown indicating the average direction of colony movement. The length of the vector can range from 0 for movements that are uniformly scattered to 1·0 if all movements are in the same direction relative to the plot centre. The *v* statistic can also range from 0 to 1·0, and represents the component of the average vector of movement projected onto a line pointing towards 0 degrees (Batschelet 1981). Thus, the *v* statistic represents the tendency of colonies to move towards the centre of the plot. The number of colony relocations per plot ranged from 1 to 14 per year.

For the experimental plots, the directions of movements clustered towards the centre of the plots in the first, second and fifth years, consistent with a tendency

Table 1. Logistic regression analyses of the probability of colony survival as a function of colony biomass (log-transformed), treatment, and plot. Model descriptions are indented below the simpler model against which they were tested. The *G*-statistic and associated *P*-value show whether the inclusion of the additional term significantly improved the fit of the model

Year	Model	Log-likelihood	G	d.f.	P
1	Constant only	−25·02			
	Constant + mass	−21·80	6·44	1	0·01
	Constant + mass + treatment	−21·73	0·15	1	<0·975
	Constant + mass + plot	−17·31	8·83	9	<0·5
	n = 50 colonies				
	Hosmer–Lemeshow goodness-of-fit statistic = 1·09; P = 0·78				
2	Constant only	−30·61			
	Constant + mass	−12·89	35·43	1	0·0000
	Constant + mass + treatment	−12·30	1·18	1	<0·5
	Constant + mass + plot	−5·59	13·43	9	<0·5
	n = 57 colonies				
	Hosmer–Lemeshow goodness-of-fit statistic = 0·81; P = 0·85				
3	Constant only	−41·05			
	Constant + mass	−29·57	22·98	1	0·0000
	Constant + mass + treatment	−28·43	2·28	1	<0·5
	Constant + mass + plot	−24·89	7·06	11	<0·9
	n = 74 colonies				
	Hosmer–Lemeshow goodness-of-fit statistic = 1·87; P = 0·60				
4	Constant only	−39·62			
	Constant + mass	−28·49	22·27	1	0·0000
	Constant + mass + treatment	−28·31	0·35	1	<0·9
	Constant + mass + plot	−21·52	13·58	11	<0·5
	n = 73 colonies				
	Hosmer–Lemeshow goodness-of-fit statistic = 0·42; P = 0·94				
5	Constant only	−37·53			
	Constant + mass	−26·80	21·46	1	0·0000
	Constant + mass + treatment	−26·21	1·17	1	<0·5
	Constant + mass + plot	−21·33	10·93	11	<0·5
	n = 75 colonies				
	Hosmer–Lemeshow goodness-of-fit statistic = 6·44; P = 0·09				

to move into areas from which neighbours have been removed. Colonies on control plots never showed significant tendencies to move towards the centre of the plot (Fig. 5).

(3) Net movement of ant biomass

During the first year of the experiment, net influx of colony biomass into the core areas of the plots was significantly higher on experimental plots (mean ± SE: 167 g ± 74, $n = 5$) than on control plots (−7·7 ± 7·7; $n = 5$; Mann–Whitney $U = 4·0$, $P < 0·05$). Negative values indicate a net outward movement of ant biomass. For the remaining years, biomass flux was much lower in experimental plots and did not differ from that in control plots (year 2: 5·5 ± 17·7 g vs. −17·4 ± 16·4 g; $U = 8·0$, $n = 5$ and 5, $P = 0·33$, NS; year 3: −6·7 ± 20·9 g vs. −31·1 ± 25·1 g; $U = 11·0$, $n = 6$ and 6, $P = 0·21$, NS; year 4: −11·2 ± 13·2 g vs. 4·8 ± 29·0 g, $U = 20·0$, $n = 6$ and 6, $P = 0·75$, NS; year 5: 18·7 ± 21·7 g vs. −11·4 ± 11·4 g, $U = 12·5$, $n = 6$ and 6, $P = 0·35$, NS).

The effects of experimental removals on the net movement of colonies was not detectable 9 m further from the core areas; that is, across an imaginary circle with a radius of 27 m. The net influx of biomass 27 m from the plot centres was never large and was never significantly higher on experimental plots than on control plots. In the third year, the influx of colonies at this distance was significantly greater on control plots (56·8 ± 20·3 g) than on experimental plots (−10·6 ± 10·6 g; $U = 15·0$, $n = 6$ and 6, $P < 0·01$). In all other years, the influx on experimental plots did not differ from that in control plots (year 1: −3·8 ± 26·6 g vs. 9·0 ± 22·0 g; $U = 15·0$, $n = 5$ and 5, $P = 0·59$, NS; year 2: 14·4 ± 14·4 g vs. 21·1 ± 29·3 g; $U = 13·0$, $n = 5$ and 5, $P = 0·91$, NS; year 4: 26·2 ± 15·3 g vs. 18·3 ± 26·4 g; $U = 18·0$, $n = 6$ and 6, $P = 1·0$, NS; year 5: −4·7 ± 24·3 g vs. 19·7 ± 22·7 g; $U = 21·0$, $n = 6$ and 6, $P = 0·63$, NS).

COLONY GROWTH RATES

Colony growth patterns are shown in Fig. 6 and associated statistical tests are summarized in Table 3. The analyses are based on regressions of colony mass at the end of the year against colony mass at the beginning of the year. Preliminary tests revealed no significant interactions between initial colony mass and treatment in any year (P-values ranged from 0·23 to 0·75). No

Table 2. Log-likelihood analysis of the probability of colony movement. Model descriptions are indented below the simpler model against which they were tested. The G-statistic and associated P-value show whether the inclusion of the additional term significantly improved the fit of the model

Year	Model	Log-likelihood	G	d.f.	P
1	Constant only	−39·94			
	Constant + treatment	−37·79	4·31	1	0·04
	Constant + treatment + mass	−37·72	0·13	1	<0·75
	Control plots				
	Constant	−17·70			
	Constant + plot	−16·83	1·74	5	0·88
	Experiment plots				
	Constant	−20·08			
	Constant + plot	−16·69	6·79	5	0·24
	$n = 60$ colonies				
2	Constant only	−36·05			
	Constant + treatment	−35·83	0·44	1	0·51
	Constant + mass	−36·05	0·0001	1	0·99
	Constant + plot	−33·53	5·03	9	0·83
	$n = 55$ colonies				
3	Constant only	−41·88			
	Constant + treatment	−41·32	1·13	1	0·29
	Constant + mass	−40·80	2·16	1	0·14
	Constant + plot	−35·38	13·01	11	0·29
	$n = 70$ colonies				
4	Constant only	−47·47			
	Constant + treatment	−46·66	1·63	1	0·20
	Constant + mass	−46·80	1·35	1	0·25
	Constant + plot	−41·82	11·3	11	0·42
	$n = 69$ colonies				
5	Constant only	−44·14			
	Constant + treatment	−44·04	0·11	1	0·74
	Constant + mass	−43·09	2·07	1	0·15
	Constant + plot	−40·43	7·43	11	0·76
	$n = 74$ colonies				
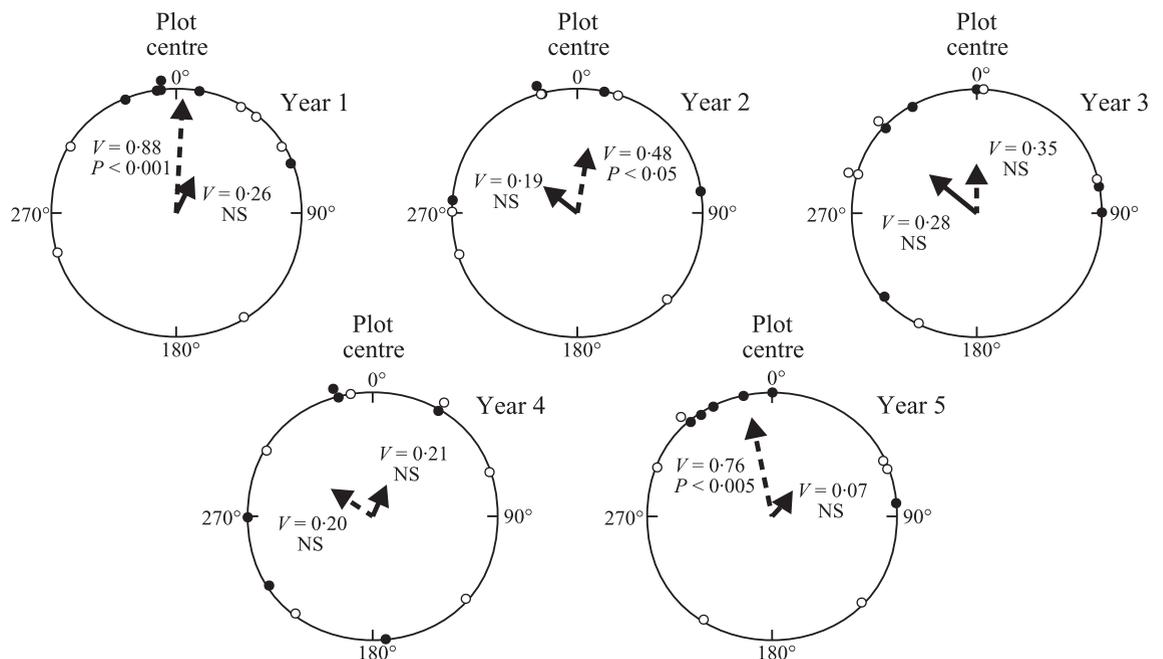
Fig. 5. Directional tendencies of colony movement. Symbols on the perimeter of the circle indicate the angle of the average vector for colony movements on an experimental plot (solid circles) or a control plot (open circles). Movement towards the centre of the plot is indicated by an angle of 0 degrees. For each year, the average vector is shown for experimental plots (dashed arrows) and for control plots (solid arrows) along with the associated v-statistic and P-value.

Table 3. Analysis of the effects of the experimental treatment on final colony mass (g) for each study year. Initial colony mass was treated as a covariate

| Source	Sum of squares	d.f.	Mean square	F	P
Year 1					
Original mass	24522	1	24522	232·7	0·0000
Treatment	3230	1	3230	30·7	0·0000
Error	3583	34	105		
Multiple $R^2 = 0.88$					
	n		Adjusted least squares means		SE
Colonies on control plots	23		65·8		2·1
Colonies on experimental plots	14		85·1		2·7
Year 2					
Source	Sum of squares	d.f.	Mean square	F	P
Original mass	22034	1	22034	51·8	0·0000
Treatment	3816	1	3816	9·0	0·004
Error	19579	46	426		
Multiple $R^2 = 0.55$					
	n		Adjusted least squares means		SE
Colonies on control plots	27		58·9		4·0
Colonies on experimental plots	22		76·8		4·4
Year 3					
Source	Sum of squares	d.f.	Mean square	F	P
Original mass	26723	1	26723	118·5	0·0000
Treatment	427	1	427	1·9	0·17
Error	12404	55	226		
Multiple $R^2 = 0.70$					
	n		Adjusted least squares means		SE
Colonies on control plots	28		51·0		2·9
Colonies on experimental plots	30		44·4		2·8
Year 4					
Source	Sum of squares	d.f.	Mean square	F	P
Original mass	4739	1	4739	11·3	0·0015
Treatment	0·5	1	0·5	0·001	0·97
Error	21016	50	420		
Multiple $R^2 = 0.18$					
	n		Adjusted least squares means		SE
Colonies on control plots	26		49·3		4·0
Colonies on experimental plots	27		49·5		3·9
Year 5					
Source	Sum of squares	d.f.	Mean square	F	P
Original mass	320472	1	30472	93·9	0·0000
Treatment	537	1	537	1·7	0·20
Plot (treatment)	9114	10	911	2·8	0·009
Error	14608	45	325		
Multiple $R^2 = 0.72$					
	n		Adjusted least squares means		SE
Colonies on control plots	28		63·3		3·6
Colonies on experimental plots	29		63·3		3·5

significant effect of plot was found in the first four years (*P*-values ranged from 0·34 to 0·71), but the identity of the study plot significantly affected final colony mass in the fifth year (Table 3). In all years there was a highly significant effect of initial colony mass on final colony mass. Taking this effect into account, final colony sizes were significantly higher on experimental plots than on control plots in the first two years, but not thereafter. The adjusted mean final mass of colonies on control plots was 77% that of colonies on experimental plots in both the first and the second year of the study. In the remaining years, the adjusted mean final masses of col-

onies did not differ significantly between experimental and control plots. In the fifth year of the study, when there were significant effects of plot on final colony size, the main effects of the treatment were not significant (Table 3).

Discussion

DENSITY-DEPENDENT POPULATION REGULATION IN *S. INVICTA*

The population dynamics of *S. invicta* observed in this study provide strong evidence for density-dependent
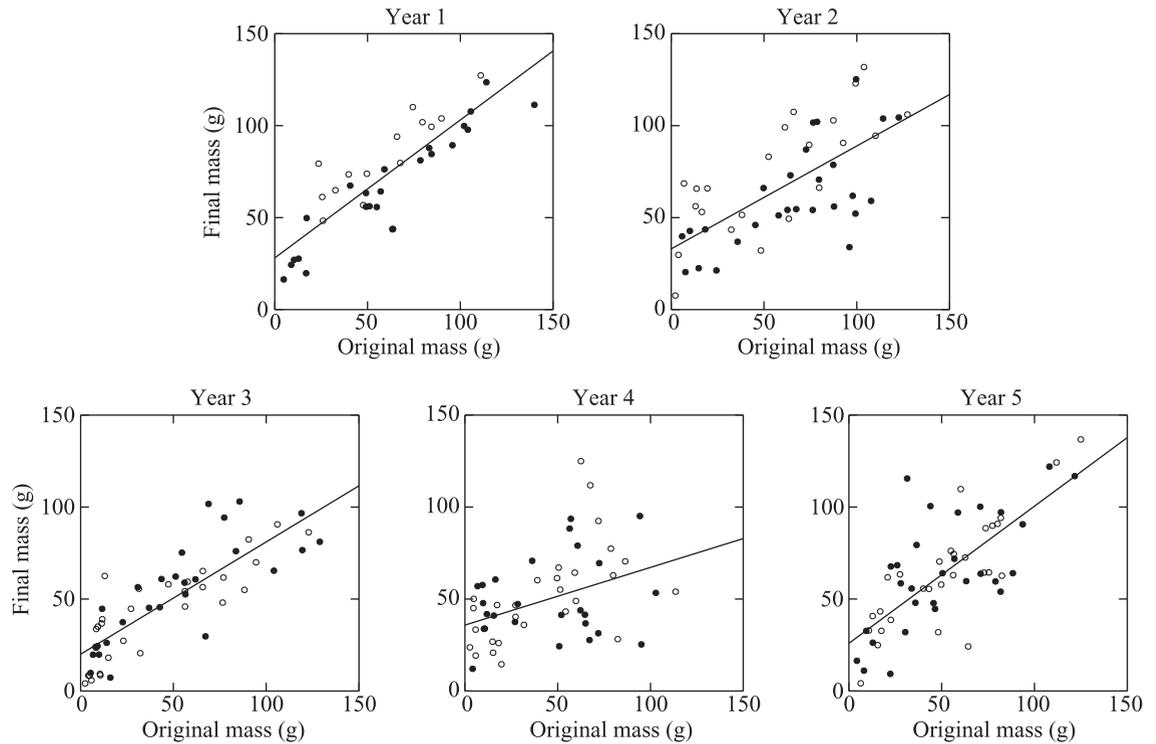
Fig. 6. Final colony mass plotted against initial colony mass for each year of the study. Colonies on experimental plots are indicated by open circles; colonies on control plots by solid circles. Growth rates of colonies on experimental plots were significantly higher than on control plots in the first 2 years.

regulation of ant biomass. There was a clear tendency for experimentally altered populations to return to levels characteristic of undisturbed populations (Fig. 1) and then to show nearly identical seasonal and annual fluctuations. Populations subject only to density-independent processes are not expected to show these trends (Murdoch 1970). Furthermore, the mean density of ant biomass on control plots varied little from year to year. Ant biomass did not vary significantly among the six annual censuses of control plots performed in late spring (square symbols in Fig. 1). The larger fluctuations apparent at other times of the year (circular symbols in Fig. 1) are in part because these other censuses were not conducted at standardized dates and because colonies of *S. invicta* undergo substantial changes in colony size through the yearly cycle (Tschinkel 1993).

Before the convergence of densities on experimental and control plots can be concluded to indicate population regulation, an alternative explanation must be ruled out. If individuals move to areas that are comparatively sparsely occupied, this can cause densities on perturbed sites to approach those on control sites even if the total density of the region containing these sites fluctuates in a density-independent manner. Thus, spatially density dependent processes do not indicate population regulation (Harrison & Cappuccino 1995). Our study plots were all situated in an open field lacking barriers to colony movement, and ant colony movement was one of the mechanisms responsible for population change. However, the effects of the experi-

mental perturbations on colony movement were very local, confined to within 9 m of the region from which colonies were removed. Furthermore, there was no detectable effect of colony removals on the biomass or number of colonies in the surrounding annuli (Figs 1b and 2b). This means that the impact of colony removals affected the movement only of immediate neighbours and perhaps of some colonies in the next tier of neighbours. The restricted effects of colony movement and the stable levels of ant density at spring censuses support the hypothesis that the *S. invicta* population is regulated by locally acting density dependent processes.

Some possible sources of error or bias should be mentioned. Estimates of colony biomass are subject to error; for example, if the plots were censused following a period of unusually low rainfall, reduced erosion of the nest-mounds could produce inflated measurements of nest size across all plots. Such occasional biases may have increased the variance in total biomass estimates across years; however, this problem was minimized by measuring only the occupied portions of the each nest-mound. It is also likely that changes in nest-mound volume lagged behind changes in the number of ants within colonies. Our estimates of total ant biomass are conservative because they are based on excavations and sampling from nest-mounds (Tschinkel *et al.* 1995) and therefore omit workers outside the nest. In addition, although we tried to place the replicate plots within similar areas of pasture, there may have been environmental differences among plots that affected ant density. For example, both colony number and ant

biomass on the outer annuli were higher on experimental plots than on control plots from early 1994 to early 1996 (Figs 1b and 2b). However, even the largest of these differences was not statistically significant when *P*-values were adjusted by Bonferroni's correction for the number of censuses performed. Furthermore, none of these sources of variation or error would produce convergence between biomass estimates on experimental and control plots in the absence of population regulation.

In much of this paper, we emphasize the density of ant biomass rather than the density of colonies. This is because the impact of ants on other species, including humans, is likely to be associated with their total number or mass, rather than with colony number *per se*. Colony densities on experimental plots converged on those of control plots; however, data on colony densities can give a misleading picture of population dynamics and regulation. For example, the graph of colony densities in core areas (Fig. 2a) appears to show that experimental plots recovered within 1 year, and may even have temporarily overshot the controls, suggesting overdamping. But the graph of total ant biomass within the same regions (Fig. 1a) shows that the recovery took approximately 2 years, with no indication of overdamping. The difference can be attributed to the burst of small colonies established in experimental plots shortly after the removals (Fig. 3). Furthermore, biomass density on control plots did not change significantly from year to year, while colony number did (Figs 1 and 2). The reason for the discrepancy is that in years with comparatively high densities of colonies, many of the colonies were very small. In general, one cannot determine the nature of population dynamics from data on colony densities alone. The same point has been made for plant populations, which also show large variation in size among adults (Harper 1977). Whereas plant ecologists have made great progress in describing the correlated changes in density, sizes, and spatial pattern that occur when plants compete (Harper 1977; Silvertown & Doust 1993), we are only beginning to establish similar quantitative rules for ants or other social insects.

Several lines of evidence indicate that the mechanism of population regulation in our study was intraspecific competition for foraging space. Colonies of the monogyne form of *S. invicta* defend exclusive foraging territories (Wilson, Dillier & Markin 1971; Tschinkel *et al.* 1995; Adams 1998). At our study site, *S. invicta* was by far the most common ant; its territories covered nearly all available habitat and the baits used to map territory boundaries were rarely occupied by other ant species. When colonies were removed, surviving neighbours expanded their territories into the vacated regions. No significant predation or parasitism of ant colonies was noted. Nests were occasionally damaged by ninebanded armadillos, *Dasypus novemcinctus*, but like many other vertebrate predators of ants, these did not kill colonies, but rather grazed, probably removing

brood or alates before these vulnerable stages were moved deep below ground and the less palatable workers rushed to defend the nest. Further evidence of the role of intraspecific competition in *S. invicta* has come from experimental studies of interactions among incipient colonies (Adams & Tschinkel 1995a, 1995b, 1995c) and of attacks by mature colonies on founding queens (Jerome *et al*. 1998).

S. invicta is not native to the United States. Like many other introduced pests, its elevated abundance suggests that it has escaped control mechanisms present in its natural range, which is principally in Brazil and Argentina. Average densities of *S. invicta* in the southeastern United States are greater than in Brazil, possibly because of escape from natural enemies (Porter *et al*. 1997). The mechanisms of population regulation in South America may differ importantly from those documented in this study; indeed, this is the hope of attempts to control *S. invicta* in the United States by biological control (Orr, Seike & Gilbert 1995). In contrast to many, but not all, non-social insect pests (Turchin 1990), the abundance of *S. invicta* is remarkably stable. This may reflect the profound differences in the biology and ecology of social and non-social insects. Due to their capacity to store resources and to alter the number of immature forms and of workers, insect colonies are buffered from brief environmental changes. Ant colonies are also perennial with long generation times. Considerable evidence indicates the importance of intra- and interspecific competition in ant populations (Hölldobler & Wilson 1990), while solitary insects are more commonly controlled by predators, parasitoids or parasites (Strong, Lawton & Southwood 1984).

MECHANISMS OF POPULATION RECOVERY

Having shown that the population is regulated by density-dependent processes, it is of interest to determine more precisely the mechanisms producing stability. There are potentially four ways that the population can recover from experimental removals: (1) by an increase in the rate of establishment of new colonies, (2) by a decrease in colony mortality rates, (3) by increased movement of colonies into the affected areas or (4) by increased colony growth. By comparing experimental and control plots, we found evidence for three these mechanisms – all except for reduced colony mortality.

More new colonies were successfully established in core areas on experimental plots than on control plots during the first year following the removals. Because new colonies become visible only after several months of growth, our measure of new colony establishment includes only those colonies that survived a gauntlet of early challenges. The large number of alate queens produced per year by mature colonies (Tschinkel 1993) contrasts with the small number surviving to the end of each study year (Fig. 3), indicating that the early mortality of mated queens or incipient colonies is prodigious. Previous studies have shown that the primary

source of mortality is attack by workers from mature colonies, which hunt and kill small colonies below ground (Nichols & Sites 1991; Jerome *et al*. 1998). The experimental removals lowered the density of such workers, which is presumably why more colonies survived long enough to produce visible nest-mounds. Reduction of competition for food may also have played a role. Similar processes are indicated in several species of desert ants for which the rate of establishment or survival of new colonies is higher at greater distances from mature colonies (Hölldobler 1976; Ryti & Case 1988; Wiernasz & Cole 1995; Gordon & Kulig 1996).

There was no evidence that the size-specific pattern of colony mortality was altered by experimental removal of competitors (Table 1). However, the annual probability of death decreased with colony size (Fig. 4) and colonies whose competitors were removed had higher growth rates (Fig. 6; Table 3). Therefore, it is possible that removal of competitors increases the probability of survival in the long term by allowing colonies to grow to safer sizes. The analysis of size-specific mortality excluded the smallest colonies, which have been shown to have density-dependent mortality rates in other contexts (Adams & Tschinkel 1995a, 1995b, 1995c). Similar patterns have been reported for ants in the genus *Pogonomyrmex*. In *P. occidentalis*, colonies closer to their nearest neighbours were more likely to die over a 1-year period, but this pattern was due primarily to mortality of newly established colonies. Mortality rates of larger colonies were less affected by spacing, but declined with colony size (Wiernasz & Cole 1995). Correlational evidence from *P. barbatus* also showed little association between the probability of death of established colonies and the local degree of crowding, despite evidence that these colonies compete (Gordon & Kulig 1998).

Much of the early increase in colony biomass in core areas of experimental plots was due to relocation of colonies from surrounding areas. Colonies near the core areas of removal plots were more likely to relocate than those on control plots (Table 2) and showed a strong tendency to move towards the centre of the plot (Fig. 5). The probable mechanism is that territories expand when neighbours are removed (see also Adams 1998), so that if a colony relocates within its territory, it is likely to move towards regions in which neighbours have died. The reappearance of a significant directional tendency on experimental plots in the fifth year of the study is surprising, given the lack of such a trend in the third and fourth years (Fig. 5). Since all other comparisons between control and experimental plots suggest that the experimentally perturbed populations had completely recovered by 2 years following the colony removals, it seems unlikely that an effect on the direction of colony relocations remained in the fifth year, despite the low *P*-value. Some studies on other ant species have also found that colonies tend to move away from competitors; for example, they may increase the distance to the nearest neighbour (De Vita 1979; but

see Gordon 1992). In our study, the effect of this tendency was a net influx of ant biomass for 1 year into the areas in which colonies had been removed. The tendency of colonies to move away from competitors may also explain why the spatial distributions of nests is clumped for incipient colonies, but often significantly regular for mature colonies (Adams & Tschinkel 1995b).

For 2 years following the experimental removals, colonies in and around the core areas of experimental plots had higher growth rates than colonies on control plots. Figure 6 shows that growth rates were elevated on experimental plots across the entire range of colony sizes. These graphs also imply that small colonies grow at higher rates than larger colonies. This confirms growth patterns inferred by Tschinkel (1993) on the basis of excavations of colonies of various sizes throughout a single annual cycle. Tschinkel showed that the decline in growth rates of larger colonies is caused by an increased rate of production of alate reproductives, which depart from the colony during mating flights (Tschinkel 1993). Since the production of alate reproductives increases with colony size in *S. invicta* (Tschinkel 1993), it can be inferred that colonies for which competition was experimentally reduced achieved higher rates of reproduction as a consequence of growth. Competition depresses reproduction in other ant species as well. For example, in the harvester ant *Pogonomyrmex barbatus*, the number of alate reproductives produced per colony was negatively associated with distances to nearby colonies in one year (Gordon & Wagner 1997) but not in another (Wagner & Gordon 1999). The ant *Lasius flavus* increased production of sexuals in response to removal of a second species of ant, showing that interspecific competition can also affect reproduction (Pontin 1961).

The density-dependent changes in colony establishment, growth, movement and mortality can be summarized by assessing their relative contributions to population recovery following the experimental perturbations. During the first year following the removals of colonies from experimental plots, colony numbers rose an average of 13·6 more in core areas of these plots than in control plots. This can be partitioned into three sources: 70% was due to the greater number of new colonies that survived to the end of the year, 18% to increased migration of colonies from surrounding regions, and 12% because there were fewer deaths in experimental plots than in control plots (since there were no colonies initially present in core areas of experimental plots). The relative contributions of these processes to biomass recovery were quite different. The average biomass of ants in core areas of experimental plots increased 362 g more than in control plots during the first year. Differences in colony movement accounted for 175 g and the greater rate of new colony establishment for only 135 g. Core areas of control plots lost an average of 81 g due to colony deaths and gained an average of 28 g due to the growth of surviving colonies during the same period.

By the beginning of the second year following the experimental removals, average colony density in experimental plots had already risen above that in control plots (Fig. 2a), but total biomass had not yet completely recovered. During the second year, the average total mass of fire ants in core areas of experimental plots rose 171 g more than in control plots, completing the recovery. Most of this increase (157 g) was due to the greater total growth of colonies that were present for the entire year. In addition, average total mass in core areas of experimental plots increased relative to control plots by 23 g due to net colony immigration and by 38 g due to new colony establishment. The total loss of mass due to colony deaths was greater in experimental plots by an average of 47 g, although the probability of colony mortality was not significantly affected by the treatment (Table 1). Since the effects of reduced competition on colony movement were local, the relative importance of density-dependent establishment, migration and growth undoubtedly depends on the size of the area from which colonies were removed. However, the responses to our experimental treatment indicate that changes in colony growth rates contribute importantly to ant population dynamics in ways that are not revealed by monitoring only the number and locations of ant colonies.

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