BIOL2131 Review of Journal Article (Adams & Tschinkel, 2001)

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1 Introductory Concepts

A population parameter is density dependent if it changes in response to the density of individuals (or, in modular organisms, modules). For example, individual mean weight is density dependent if it decreases with increasing density. Many phenomena are naturally density dependent, for example the frequency of signaling behaviour (if there is nobody to signal to, there's no point). However, density dependence in the fundamental processes of birth and death is important because it can keep a population stabilised to within a density range. This is known as population regulation.

At high enough densities, population regulation will always come into effect, if only because there is physically not enough space for any more individuals. This is an extreme case of intra-specific competition: competition within a species for an essential resource that is in limited supply (Begon *et al*, 1996, p. 214). In general, the higher the density of a population, the more intra-specific competition will occur, i.e. it is density dependent. The feedback that results imposes a limit on the natural (exponential) rate of increase.

The effect of intra-specific competition depends on the behaviour of the species. If individuals compete with each other only indirectly, through their consumption of a limited resource, and whatever available resources are effectively shared, there will be a critical density at which each's 'ration' is not enough to survive on. This case is known as 'exploitation' or 'scramble' competition, and results in a population crash at high density. The other extreme is when individuals actively prevent others from exploiting their resource allocation, often by defending territory. In this 'interference' or 'contest' competition, any extras above the density at which there are no spare resources will be denied the essential resource and will die; thus the population will return to the equilibrium density (carrying capacity). In reality a population response will be somewhere between these two.

The descriptions just given were of density dependent mortality, but the same principle applies to fecundity and growth; for that reason it is often better to use the general terms of 'overcompensating density dependence' for scramble-like competition, and 'exactly compensating density dependence' for contest-like competition (Begon *et al*, 1996, p. 218).

It is a central idea in ecology that population regulation is a result of density dependent processes, especially intra-specific competition. However this is not universally accepted–some think the evidence is not clear and that density independent processes could be often more significant. Eldrige S. Adams and Walter R. Tschinkel tested population regulation processes as they relate to fire ants as reported in the paper "Mechanisms of population regulation in the fire ant *Solenopsis invicta*: an experimental study" (Adams & Tschinkel, 2001). The remainder of this essay summarises their paper.

2 Overview of the Study

In comparison to non-social insect species, there has not been much experimental work done on the population dynamics of social insects. As a result, predictive models of this widespread group could be better and have not been sufficiently validated. One aim of this study was to provide clear data on the dynamics of an ant population, measuring various processes in one study so that they can be compared.

This study was a convergence experiment, which can be used to detect density dependence. A natural population is disturbed (by increasing or decreasing density) and then censused regularly to observe its response. Control plots are also censused. If the experimental population dynamics converge on the control population dynamics, we can conclude that they are regulated by density dependent processes. The power of this approach is that it can detect density dependence even when there are strong density independent processes occurring (environmental factors). It is important to note that this does not imply that the primary regulating factor is intra-specific competition–other processes such as predation or parasitism can also regulate populations.

3 Synopsis of Methods

The study was conducted on an open population of fire ants in pasture in Florida, USA. Colonies were killed in the central areas of 6 experimental plots. Over the following 5 years, these plots (the central and surrounding areas) and 6 control plots were censused at a specific time of year, as well as irregular times in between. The number of colonies was measured, their position and the estimated ant biomass within.

The length, width and height of nest mounds was measured, then volume approximated by an equivalent ellipsoid. This correlates with ant biomass, as was calibrated previously, but is conservative because it excludes foragers. Only nests of at least 0.5L were counted. Each nest was poked with a long wire to determine whether it was occupied.

The territory size of representative colonies was mapped before and for 2 months after the experimental removals. 2 nests adjacent to the central area were selected from each of 3 experimental (disturbed) and 3 control plots. Baits were placed around these nests and aggression between foragers was noted. The area bounded by bait sites where aggression occurred was defined as the territory of the colony.

Time series were constructed from the raw data, including: establishment of new colonies, colony mortality, colony movement vectors, and colony growth.

4 Results

Mean ant biomass in the central (cleared) areas of experimental plots converged on the mean biomass in central areas of the control plots. They were not significantly different after 2 years (see Figure 1). Biomass in the surrounding areas was never significantly different from controls. The number of new colonies established in the first year after removal was significantly more in central areas of experimental plots than controls, but not for the other years. (see Figure 2)

The probability of colonies surviving to the end of the year correlated with nest size. This did not differ between years, plots, or according to experimental treatment.

Colonies on experimental plots were significantly more likely to move than those on control plots in the first year after experimental removal. In the first two years the average movement vector was weighted significantly towards the centre of the plot. In the first year there was significant movement of biomass into the central areas of experimental plots, from the adjacent surrounding areas.

In all years growth rates were inversely proportional to nest size. Taking this into account, colonies in central areas of experimental plots had a significantly higher growth rate than those on control plots, for 2 years after removal.

In the 8 weeks after disturbance, territories adjacent to removal in experimental plots expanded significantly, more than doubling in size on average. No significant change affected equivalent nests on control plots.

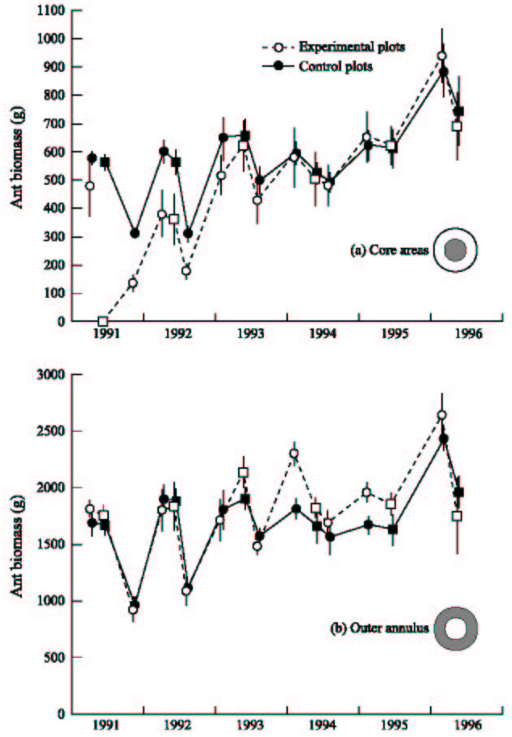

Figure 1: Biomass. Measurements taken before removal are shown unconnected at left. The top graph shows areas that were cleared in the experimental condition, the bottom graph shows data for the surrounding areas (3 times the area). Square points indicate standard annual census dates. Much of the intervening variation is due to an annual population cycle. (Adams & Tschinkel, 2001)

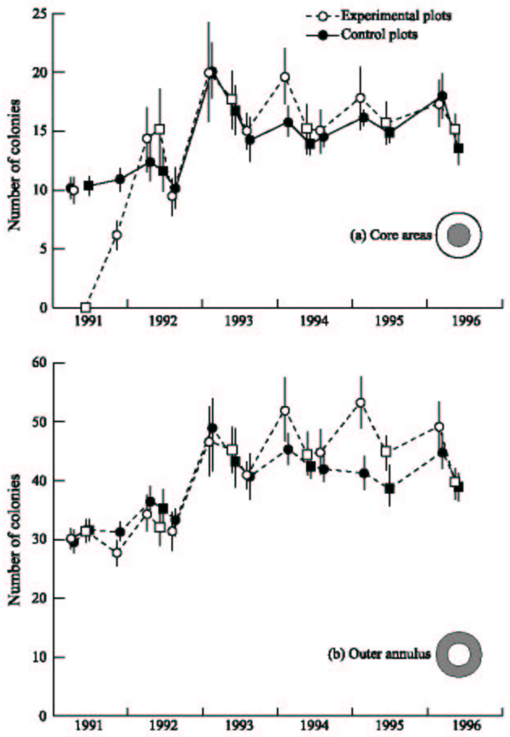

Figure 2: Colonies. See Figure 1 for notes. (Adams & Tschinkel, 2001)

5 Discussion

The ant populations in experimentally removed areas returned gradually to the levels in control plots. Within 1 year the number of colonies had returned to the normal level, through increased nest founding and movement, but the biomass was still reduced. With increased growth rates the colonies increased in size and attained indistinguishable biomass density within 2 years. For the remaining 3 years there was considerable variation in density over time, but the patterns were the same on experimental and control plots. Thus convergence occurred, indicating that the populations are regulated by density dependent processes. The pattern is consistent with exactly-compensating density dependence.

There is an alternative possibility. If the density dependent processes are only spatially acting, i.e. movement of the total remaining population towards underpopulated areas, this can lead to convergence even though total density is not regulated. Indeed, there was a movement tendency towards the centre, but importantly this was limited to within 9m of removal areas. The incoming biomass was not enough to significantly decrease biomass in the surrounding areas (the source of inflow). Since the density in surrounding areas was stable between years, this suggests that density dependent population regulation is indeed occurring.

There are two measures of density involved here: colony density and biomass density. If fire ant colonies are considered as modular organisms, we should expect competition to regulate the modules (ants, i.e. biomass) rather than genets (colonies) (Begon *et al*, 1996, p. 231). The more rapid recovery of colony density can be explained by the fact that many small colonies were established in the first year; it was another year until biomass density reached a stable level.

No predation or parasitism was observed in the fire ant population; nor were there other ant species in the area. Thus it seems clear that density was regulated by intra-specific competition for foraging space. This is supported by the observation that the foraging territories of colonies adjacent to removal areas expanded into the newly available space.

In the first year after removals, the increased colony numbers in central areas of experimental plots relative to control areas can be attributed to: 70% from newly established colonies, 18% from movement of established colonies, 12% from less colony mortality (since there were no colonies anyway). However, the contributions to biomass density were very different: new establishment caused only 37% of the increase, while movement caused 48%. In the second year, 92% of the biomass increase was due to increased colony growth.

It is important to note that since the experimental effect of movement tendency is locally acting, the relative importance of the factors given above will vary according to the scale of disturbance.

Although removal of neighbours was not found to have a measurable effect on colony mortality rate, it did lead to an increased growth rate. Since it was also found that larger colonies are less likely to die, removal of neighbours (reduction of competition) may indirectly decrease mortality by allowing small colonies to grow to a safe size.

6 Mechanisms

The primary mechanism behind competition for foraging space is the aggressive defense of territory by workers. Each nest is thus restricted to a certain area from which to gather food, which limits the number of ants that can be supported (i.e. the size of the colony). However territory is divided, space and food are limited on each plot which limits the total ant biomass that can be supported.

Colonies tend to relocate within their territories, if possible, away from a near neighbour nest. This process causes local movement into a cleared area following the expansion of territory. The same mechanism is responsible for the shift from an initially random distribution to a much more evenly spaced pattern of colonies.

The results indicate that an important mechanism of population recovery is increased establishment of new colonies, which might be thought of as increased fecundity of the surrounding colonies. In fact, what is probably occurring is that the founding queens from those colonies, after their mating flights, are more likely to establish a colony that survives at least a year. Workers from existing colonies seek out and kill founding queens in their territory; since there were few such workers in the cleared area, successful establishment was more probable. Thus, the finding of no density dependent effect on mortality is contradicted in the case of incipient colonies, but it wasn't detected because only nests of at least 0.5L that survived the year were counted.

7 Management Implications

Fire ants are a pest species in many regions including parts of North America and Australia. It would be desirable economically, socially and environmentally to reduce or eliminate them.

The results show that populations of fire ants are regulated by intra-specific competition. Clearly if they are reduced by a once-off disturbance without ongoing control measures, they will return to the equilibrium density fairly rapidly. In small scale cases this would be driven by movement of existing colonies; on larger scales, increased rates of colony establishment would be more significant.

It should be noted that there are two forms of *S. invicta*: in the monogyne form there is one reproductive queen per colony and territory is defended from neighbours; in the polygyne form there can be many queens in one nest and workers from neighbouring nests intermingle without aggression. Additionally nests can merge into each other without a clear distinction. The population dynamics described here only apply to the monogyne form (found at the study site).

Social insect populations seem to be generally more stable than non-social insect species. They are more likely to be 'self-regulating' via intra- or inter-specific competition. They can withstand environmental variation by storing food and controlling their age structure and class structure. Additionally they typically have longer generation times than non-social insects. These factors probably insulate the populations from short-term chaotic dynamics often seen in other species, and thus statistical population models could potentially give reliable predictions.

The equilibrium densities of *S. invicta* in places where it is an introduced pest are generally higher than in its native regions of Brazil and Argentina. This suggests that it may be naturally regulated by additional mechanisms such as inter-specific competitors, predators, parasites, or disease. If these could be safely introduced to the pest-infested regions, they may reduce the density–and thus impact–of fire ants.

8 References

1. Adams, E. S. & Tschinkel, W. R. (2001). Mechanisms of population regulation in the fire ant *Solenopsis invicta*: an experimental study. *Journal of Animal Ecology* 70, 355-369.

2. Begon, M., Harper, J. L. & Townsend, C. R. (1996). *Ecology* (Third edition). Blackwell Science.