# Social breakdown as a population regulating process in invasive ant species.

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**Abstract:** Studies of invasive species have frequently recorded explosive population growth, often followed by decline. Causes of population stabilisation have rarely been explicitly identified; general mechanisms proposed have included intrinsic population dynamics and predators, parasitoids or pathogens attack. Some of the most harmful invasive species in terms of impacts on natural ecosystems are super-colony forming ants. Population processes within such colonies are of great importance to biodiversity conservation and the invasive species management. These super-colonies have only been reported from the invasive range and in their natural range the ants form small, dispersed colonies: low genetic variation in the introduced populations may facilitate super-colony development. The development of a 101 hectare crazy ant *Anoplolepis gracilipes* super-colony has been studied: by 2004 this had fragmented into 10 small isolated colonies. Here I show that colony breakdown was caused by intra-colonial social fragmentation, which will lead to the development of the low density, dispersed characteristics of natural colonies; this has notable implications for the control of invasive ant colonies and their impacts on biodiversity.

**Keywords:** *Anoplolepis*, Formicidae invasion, population structure, Seychelles

The crazy ant *Anoplolepis gracilipes* (Smith, 1857) is regarded as one of the world's most invasive species, being listed as one of the 100 'worst alien species' (Lowe *et al*. 2001). It forms super-colonies where a large geographical area is occupied by a single colony with multiple queens or by numerous colonies that interact and operate as a single unit (Tsutsui & Suarez 2003). These invasive super colonies have caused significant destruction of animal populations on tropical islands, most famously including significant reductions in the populations of land crabs on Christmas Island (Green *et al*., 1999). In the Seychelles islands crazy ants have been present since 1962 (Haines & Haines 1978). By 2004 they were established on 11 islands (Mahé, Anonyme, St. Anne, Praslin, Curieuse, Cousin, Petite Soeur, Felicite, Marianne, La Digue and Bird island – Gerlach 2004 and unpublished data). Population expansion on Bird island caused high levels of mortality to the globally important nesting colony of sooty terns *Sterna fuscata* (Feare 1999). Impacts on invertebrates and the pattern of colony expansion were studied in 2001-2 (Gerlach 2004). The island was found to be completely covered by a single super-colony of the ant by 2002, with population densities of 60m$^{-2}$ (Gerlach 2004). From this the total ant population could be estimated at some 60 million individuals (Fig. 1).

**Materials and methods**

In September 2004 the distribution and abundance of ants on Bird island was investigated in a repeat of earlier studies (Gerlach 2004). 100 1$m^2$ quadrats were placed haphazardly across the island. Leaf litter in these quadrats was collected and processed through Tulgren funnels to obtain accurate data on crazy ant abundance. These methods are comparable to those used in 2001 and 2002 (Gerlach 2004), providing a direct comparison to earlier data. In addition searches were made along all paths for the presence of crazy ant colonies.

Inter-colonial intections were studied using a standard behavioural assay as in previous studies of ant inter-colonial interactions (Tsutsui & Case 2001; Giraud et al. 2002; Tsutsui & Suarez 2003). This paired two individual workers together in a neutral arena for 5 minutes. Interactions were scored as 1 = touching (without aggression, includes antennation), 2 = avoidance (one ant moving away from the other after physical contact), 3 = aggression (physical attack, includes lunging and biting) and 4 = fighting (prolonged biting and pulling, and use of chemical defences). 30 replicate trials were used pairing close nests (10m apart) and 30 pairing widely separated nests (200m apart). An additional study placed 10 worker ants (marked with a small dot of paint on the abdomen) in an arena with 10 workers from a different colony. After 15 minutes the ants were gathered into one or two groups, the composition of these groups was recorded. 10 replicates were used.

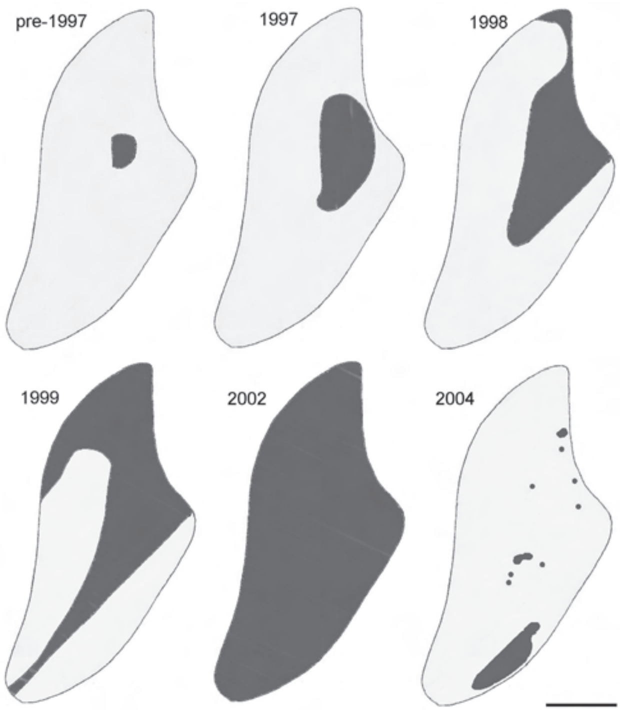


**Fig. 1.** Crazy ant distribution on Bird island 1997-2004 (dark areas). Scale bar 100m

## Results

This study recorded crazy ants in only 20% of quadrats, compared to all quadrats in 2002 (69% in 2001 when the colony was still in the process of expansion). Ant densities in the quadrats where they were present were 0.6-50m$^{-2}$ (mean 18.8m$^{-2}$), compared to 60m$^{-2}$ in 2002. 10 distinct colonies were located, covering a total of 0.0225 hectares (compared to 70ha in 2001 and 100ha in 2002). The estimated population is 26,000 individuals (a reduction of over 99% since 2002). No significant change occurred in the abundance or distribution of other ant species.

Inter-colonial interaction individual tests recorded only low levels of agonistic behaviour: individuals from adjacent nests showed behaviours 1 and 2 (1 at 7%, 2 at 93%); individuals from disparate nests showed behaviour 2 only (with one exception when aggressive behaviour 3 was observed) (Table 1). In the group tests ants from widely separated colonies had formed completely separate groups, those from adjacent colonies were largely separate, although there was a low level of overlap (5%) (Fig. 2).

**Table 1.** Behavioural interactions between ants from different colonies

| Behavioural category | Number of observations 10m apart | 200m apart |
|---|---|---|
| 1 | 2 | 0 |
| 2 | 28 | 29 |
| 3 | 0 | 1 |
| 4 | 0 | 0 |

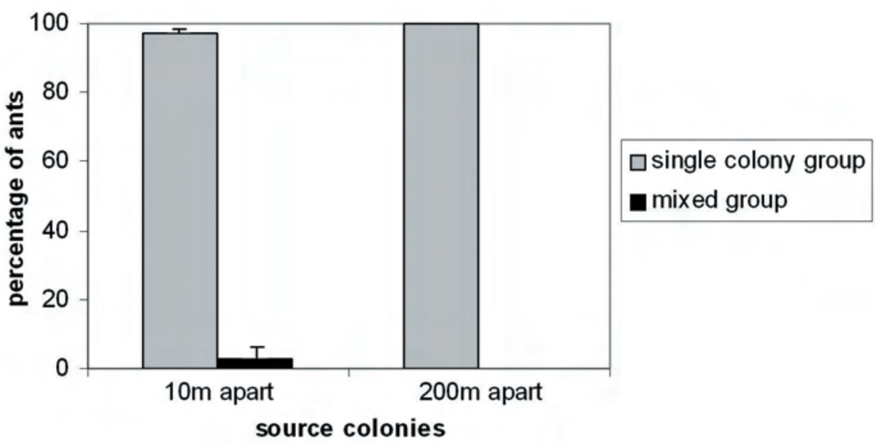


**Fig. 2.** Clustering behaviour of ants from different colonies, separating into either single colony or mixed groups

**Discussion**

The distribution pattern and the lack of interaction between workers from different colonies suggests that the super-colony that characterised the Bird island crazy ant population in 2002 has fragmented into at least 10 separate colonies. No significant aggression was observed between individuals or colonies but the low level agonistic behaviour and the avoidance of individuals from other colonies is probably sufficient to maintain colony isolation. This results in most of the island being free from resident crazy ants, foraging ants spread widely and foraging crazy ants probably cover most of the island but the impact of the ants is greatly reduced. This distribution resembles the very dispersed colony structures observed on the islands where the ants have been long established (Mahé, Praslin and La Digue) and the social fragmentation identified here may be an integral feature of population expansion in ants forming super-colonies. Other factors were not explicitly tested but there is no evidence of disease in the colonies, temperature and rainfall did not differ significantly over the study period, abundance and diversity of other ant species did not change and resource levels appeared to remain constant (as indicated by invertebrate abundance and vegetation cover).

Similar super-colonies have been reported in the Argentine ant *Linepithema humile* (Giraud *et al*. 2002; Tsutsui & Suarez 2003; Tsutsui *et al*. 2003). These form large colonies with low genetic diversity in introduced populations (Tsutsui *et al*. 2003) compared to smaller (tens to hundreds of metres diameter) (Tsutsui *et al*. 2000; Tsutsui & Case 2001), more isolated and more genetically diverse colonies in their native range which are aggressively defended from other conspecific ant colonies (Suarez *et al*. 1999; Tsutsui *et al*. 2000; Tsutsui & Case 2001). A contrast between the low density, low impact native colonies and the high density, high impact invasive supercolonies has been noted (Markin 1970; Rao *et al*. 1991; Human & Gordon 1996; Holway *et al*. 1998; Suarez *et al*. 1998; Holway 1999; Giraud *et al*. 2002; Tsutsui *et al*. 2003). It is believed that new colonies are formed by budding from the super-colony, rather than by dispersal (Tsutsui *et al*. 2003) and that the low genetic diversity of introduced populations facilitates the formation of supercolonies (Tsutsui *et al*. 2003). The findings here suggest that the difference between the multicolonial natural populations and the unicolonial introduced populations may not be due to a fundamental difference between these populations, but to the length of time they have been established. The Bird island population suggests that over time the supercolony will fragment and form a number of smaller colonies. Continued isolation of these will reduce cooperation between the colonies and a reduction in the impact of the invasive ants. Consequently in a largely stable ecosystem the highly destructive unicolonial invasive ants populations may decline to less problematic levels over time. Although few ants are unicolonial, as all the invasive species possess this colony structure (Passera 1984; Holway *et al*. 2002) this process of population regulation has major implications for ant invasions. These colonies may be highly damaging (Gillespie & Reimer 1993) as they spread but fragmentation may lead to the reduction of impacts, due not to extrinsic ecological factors but solely to social fragmentation. Given the phenomenally rapid spread of the highly invasive ant species these super-colonies may exceed their stable size relatively rapidly.

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