

Research article

Supercolonies of the invasive yellow crazy ant, *Anoplolepis gracilipes*, on an oceanic island: Forager activity patterns, density and biomass

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Summary. Ants have the capacity to reach unusually high densities, mostly in their introduced ranges. Numerical dominance is often cited as key to the ability of exotic ants to displace native ant species, reduce the abundance of invertebrates and negatively impact upon bird, land crab and other vertebrate populations. On Christmas Island, Indian Ocean, the yellow crazy ant, *Anoplolepis gracilipes* (Jerdon), forms supercolonies, where extremely high densities of foraging ants have contributed to ‘invasional meltdown’ in rainforest areas. Densities of up to 2254 foraging ants per m² and a biomass of 1.85 g per m² were recorded, and nest densities reached 10.5 nest entrances per m². Populations of *A. gracilipes* can overcome and kill red endemic land crabs (*Gecarcoidea natalis*) over 100 times their own biomass. This is the highest recorded density of foraging ants, and adds another element to the definition of ‘supercolony’ of unicolonial ants. This paper documents one extreme in a continuum of densities of unicolonial, invasive ant species and highlights the need to incorporate forager densities into invasive ant research.

Key words: *Anoplolepis gracilipes*, invasive ants, supercolony, unicolonial population, intraspecific aggression.

Introduction

Invasions by introduced alien ants repeatedly cause ecological disruption affecting both continental and island ecosystems throughout the world (Holway et al., 2002). It is often through sheer numerical dominance that invasive ants can achieve superior competitive and interference abilities and recruitment to food sources (Porter and Savignano, 1990; Human and Gordon, 1996; Holway and Case, 2001). Invasive ants sometimes reach abundances exceeding that of all native ant species combined in comparable uninvaded areas (Porter and Savignano, 1990; Holway, 1998; Hoffmann et al., 1999).

Many ant species (Holway et al., 2002), but especially invasive ants, display unicoloniality in their introduced ranges (Hölldobler and Wilson, 1990). Literally meaning ‘one colony’, foragers in these cooperative colonies do not exhibit aggression toward conspecifics within the larger colony, even toward individuals from physically separate nests (Holway et al., 1998). These populations are often referred to as ‘supercolonies’, covering large spatial scales (Giraud et al., 2002). Species of invasive ants that have been described as forming supercolonies include the Argentine ant, *Linepithema humile*, the big-headed ant, *Pheidole megacephala*, the yellow crazy ant, *Anoplolepis gracilipes* and the garden ant, *Lasius neglectus* (Erickson, 1971; Hoffmann et al., 1999; Tsutsui et al., 2000; O’Dowd et al., 2003; Espadaler et al., 2004).

Supercolonies have traditionally been defined without specific reference to the activity levels or densities of foraging worker ants. However, formation of supercolonies may facilitate rapid population increase and invasive impacts (Holway et al., 2002; O’Dowd et al., 2003). Indeed, once Argentine ants fuse into supercolonies in North America, Holway et al. (1998) argue that worker density (as opposed to mound or nest density) becomes the most ecologically meaningful measure of population size. It is the density of foraging workers that is directly responsible for invasive impacts in the environment. Considering that the densities of invasive species can actually be higher in their native range than their introduced range (Heller, 2004), for invasion biologists, the density of foraging worker ants in supercolonies is a key consideration.

The invasive yellow crazy ant, *Anoplolepis gracilipes* (formerly *Anoplolepis longipes* Jerdon), forms a mosaic of high-density supercolonies on Christmas Island, Indian Ocean, where incredibly high densities of ants are sustained 24 hours a day, all year round on the ground and in the canopy. Foraging ants in these supercolonies do not typically form trails, and their density is sufficient to kill red land crabs within

24 hours, resulting in an increase in accumulation of leaf litter and mass recruitment of seedlings (O'Dowd et al., 2003). In addition to high-density supercolonies where they kill red land crabs, isolated nests of *A. gracilipes* are widely distributed across the island and exhibit low activity levels. The genetic relatedness among these isolated nests is unknown; however, it is possible that a single related supercolony covers the entire island.

A. gracilipes was accidentally introduced to Christmas Island probably some time between 1915 and 1934 (O'Dowd et al., 1999). The first supercolony was discovered in 1989, and since 1996 supercolonies have rapidly formed and spread across island rainforest. In September 2002, 28% of the 10,000 ha of rainforest on Christmas Island was occupied by *A. gracilipes* supercolonies (Green et al., 2004). *A. gracilipes* has never been recorded to cause the magnitude of ecological impacts as seen on Christmas Island, i.e. the removal of a 'keystone' species (O'Dowd et al., 2003).

Here I use a rapid method for assessing the activity levels of foraging *A. gracilipes* in supercolonies on Christmas Island, Indian Ocean, and determine its relationship with ant density. I describe biomass, diel and seasonal activity patterns, both on the ground and on tree trunks, and nest entrance densities. Lastly, I determine levels of intraspecific aggression between and within supercolonies, and between isolated nests and supercolonies, to help resolve whether the island comprises one large, or many spatially disjunct supercolonies of the yellow crazy ant.

Methods and materials

The study system

Christmas Island (105° 40'E, 10° 30'S) is an uplifted oceanic limestone island that lies 360 km south of Java in the north-eastern Indian Ocean. The island is located in the humid tropics, and experiences a monsoonal climate where most of the 2000 mm mean annual rainfall occurs between December and May (Falkland, 1986). Approximately 74% of the island is covered with native vegetation (Mitchell, 1985), where vegetation type corresponds generally with geological substrate type (Barrie, 1967).

This study was conducted between December 2000 and December 2002 in areas of *A. gracilipes* supercolony formation. Supercolonies covered >2500 ha of the island between 2001 and 2003 (Green et al., 2004). I used eight sites for the majority of data collection in this study (Fig. 1), each consisting of a 50 m × 50 m plots (0.25 ha) in rainforest where all stems >5 cm dbh were mapped and identified (P.T. Green, unpubl. data). Five plots were in recently formed supercolonies (<1.5 years old) while at three other sites the supercolonies had been established for approximately 5 years in 2000 (P.T. Green, pers. comm.). All sites were characterised by the absence of red land crabs and a thick layer of leaf litter. The recently invaded sites were typically carpeted by small seedlings while the older sites had both small and large (~2 m tall) seedlings in the understorey.

Ant activity/density calibration

Traditional methods of determining ant abundance (e.g. pitfall trapping and standard quadrat counts) were impractical for use in *A. gracilipes* supercolonies due to such high densities of foraging ants. Pitfall traps filled up with ants within a few hours of placing them in the field.

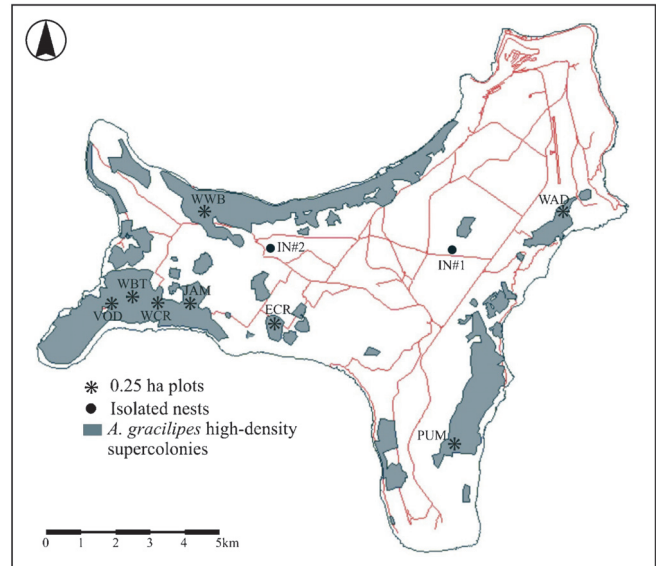


Figure 1. Distribution of *Anoplolepis gracilipes* supercolonies on Christmas Island, and locations of sites used in this study, including isolated nests used for intraspecific aggression assays. IN = isolated nest

Therefore, I developed a rapid field assessment technique for quantifying relative activity of crazy ant foragers on the forest floor. Ant activity was estimated by the number of *A. gracilipes* crossing a 10 cm × 10 cm laminated white card on the ground in 30 seconds (referred to hereafter as 'ants per 30 secs'). However, to relate ant activity to density, the two must be correlated. Hence, I collected data to determine the relationship of ant activity as recorded by ant activity cards with actual density of ants on the forest floor.

I made 63 ant activity counts in four different *A. gracilipes* supercolonies. At each point I placed a laminated white card on the ground in an area cleared of litter (diameter 30 cm) and counted the number of ants to cross the card in 30 secs. Immediately after, I placed a circular frame (0.19 m²) over the area and used a petrol-driven garden vacuum to collect all foraging ants from within the frame. Activity counts spanned a wide range of ant activity (0–145 ants per 30 secs). I used linear regression to determine the relationship between ant activity and actual ant density on the ground, and how the activity count might predict ant density.

Ant biomass and nest entrances in supercolonies

The biomass of ants on the forest floor was calculated by multiplying the density of foraging ants by the mean individual weight of an unfed worker ant. I collected worker ants with petrol-driven garden vacuum, whose gasters were not distended in any way (my subjective sorting) and for my purposes were 'unfed'. Because worker ants are extremely light, I weighed six pooled collections of ants, ranging from 20–104 individual workers each, and calculated the overall mean mass of an individual from the average worker mass in each of the six collections.

Nest entrance densities were examined in 20 3 × 3 m quadrats from four separate supercolonies. Their microhabitat distributions were inferred from the concentrations of workers streaming out of holes and cracks in the ground, from under logs, rocks and bases of trees. Queens were often found upon excavation of these sites, along with brood. I termed these 'nest entrances', but it is likely that many of these entrances were interconnected either below the surface of the ground or within leaf litter and that each one did not constitute a discrete nest. The excavation of a complete nest was almost impossible, so I quantified

entrance density. I counted the number of entrances in the quadrats at three microhabitats on the ground (holes in ground, under rocks/logs, base of a tree/root and empty holes in the ground). By counting empty holes, I could calculate the percentage of potential nest sites used, or saturation of nest sites. In addition to the quadrats, the presence of nest entrances at the base of trees (dbh >5 cm) in five entire 0.25 ha plots was recorded.

I calculated mean density of nest entrances in use by *A. gracilipes* per site and the percentage of holes in the ground utilized by *A. gracilipes* as nesting sites. I used a two-way ANOVA to investigate the effect of site and nest entrance location on the density of nest entrances. From the observations of *A. gracilipes* nests at the base of trees in the 0.25 ha plots, I determined the mean proportion of large rainforest trees that harboured *A. gracilipes* nests.

Ant activity on the forest floor and tree trunks

I recorded diel ant activity on the forest floor every hour for 24 hours on two occasions at two different sites: 21–22 February 2001 at ECR (Fig. 1; 'new' supercolony, wet season) and 23–24 August 2001 at WBT (Fig. 1; 'old' supercolony, dry season). Each hour, 20 activity counts were made at random locations within the 0.25 ha plots and a mean of those counts was used as the ant activity index for that hour. Activity of *A. gracilipes* on tree trunks was also recorded at WBT in August 2001. Eleven trunks (4 × *Inocarpus fagifer*, 2 × *Dysoxylum gaudichaudianum*, 2 × *Barringtonia racemosa*, 2 × *Celtis timorensis* and 1 × *Ligustrum glomeratum*) >10 cm dbh were chosen and a 10 cm-wide band of white acrylic spray paint sprayed around the trunk at breast height (130 cm above ground) and left to dry. The number of ants in one trail crossing a 10 cm × 10 cm band was recorded for 30 seconds each hour. Relative humidity was measured hourly using a horsehair hygrometer at breast height at ECR, and air temperature at ground level was recorded hourly at WBT. The presence of queens on the surface of the ground was also recorded for 24 hours in August by five-minute visual searches every hour.

Seasonal ant activity was recorded weekly for 19 months commencing on 6 February 2001. Ant activity was recorded in 20 random locations within 0.25 ha plots at ECR and WAD each week, between 9:00 and 12:00.

Intraspecific aggression

Workers, queens and brood were collected from intact *A. gracilipes* nests within supercolonies and from isolated nests using a petrol-driven garden vacuum. They were transferred to a lab and fed with 30% sugar solution. I conducted intraspecific aggression assays with individual workers from within the same supercolony, between supercolonies, between isolated nests, and between isolated nests and supercolonies. In most cases, assays were conducted between 12 and 48 hours after collection from the field. I carried out 10–14 trials for each of 13 combinations of nest location. Pairs of ants were placed in flouon-coated 80 ml vials (arena 40 mm diameter), and the highest level of aggression between the two ants during the interaction was recorded after 10 minutes. I used the mean of completed replicates as the level of intraspecific aggression for that combination.

Interactions were scored as: 0 = *Tolerance*, partner grooming or huddling and exchanging food; 1 = *Antennation*, initial antennation then tolerance; 2 = *Intense antennation* (investigation), rapid mutual antennation; 3 = *Avoidance or flight*, dorsal flexion for chemical defense; 4 = *Aggression*, biting or pulling legs and antennae, repeated back and forth jerking; 5 = *Fight*, prolonged aggression, sparring, charging, biting and chemical defense. Levels 0–2 are considered non-aggressive behaviour, and 3–5 aggressive (Hölldobler and Wilson, 1990). I used linear regression to investigate the relationship between the mean level of aggression and distance between nests.

Results

Ant activity/density calibration

Ant activity (ants per 30 secs) was very strongly correlated with actual forager density ($r^2 = 0.897$, $p < 0.001$; Fig. 2), and is therefore a reliable measure of ant density on the forest floor.

Ant biomass and nest entrances in supercolonies

The density of *A. gracilipes* workers on the forest floor was highly variable, but reached extremely high levels. Using the seasonal activity counts at ECR, WAD and WBT (see below), the mean ant activity count at any site varied between 6 and 145 ants per 30 secs, the equivalent of about 72–2254 ants per m² (mean 948.7 ± 31.7 SE ants per m²; 0.7 million – 22.5 million ants on the forest floor per hectare). However, the highest density actually measured using the garden vacuum was 7383 ants per m². Foraging *A. gracilipes* workers were by far the most conspicuous organism on any surface in supercolony areas.

Despite the density of workers being so high, their biomass was comparably low. Unfed ants weighed an average of 0.821 ± 0.299 mg. Consequently, the mean biomass of unfed crazy ants on the forest floor was $948.7 \times 0.0008214 = 0.779$ g per m², and ranged between 0.059 g per m² and 1.851 g per m². Even at the highest densities (and assuming all ants are unfed), the biomass of crazy ants on the forest floor was ~6.064 g per m².

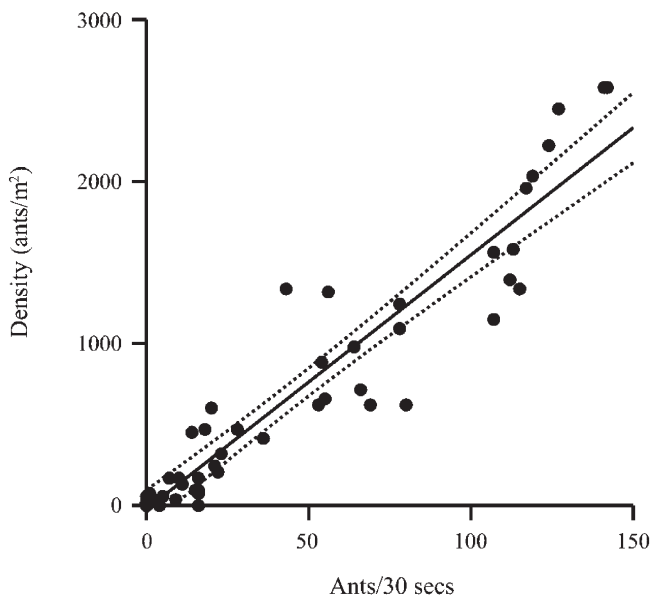


Figure 2. Density of ground foraging crazy ants in relation to ant activity on cards, as explained by the number of ants crossing a 10 cm × 10 cm white card in 30 seconds (ant activity counts). Points represent individual activity counts and samples taken with petrol-driven garden vacuum across a range of ant densities (within and outside supercolonies). Equation of the line: $y = 15.694x - 21.612$ and dotted lines are 95% confidence intervals

Table 1. (a) Mean density of nests at different microhabitat locations, and (b) percentage of rainforest trees (dbh >5 cm) harbouring nests at their base in *A. gracilipes* supercolonies. Nests at the base of trees were counted in 0.25 ha plots, and all other nest types were quantified using quadrat counts

(a) Nest entrance location	Mean nest entrances per m ² (± SE; n = 5)				
	ECR	WAD	WWB	WBT	Mean
Holes in ground	9.2 ± 1.3	1.6 ± 0.2	1.7 ± 0.3	5.1 ± 1.6	4.4 ± 1.8
Under log/rock	0.3 ± 0.2	0.8 ± 0.2	0.6 ± 0.3	0.6 ± 0.1	0.6 ± 0.1
Base of tree/root (dbh <5 cm)	0.9 ± 0.2	0.3 ± 0.1	0.6 ± 0.1	0.5 ± 0.2	0.6 ± 0.1
Total used nests	10.5 ± 1.5	2.7 ± 0.1	2.9 ± 0.4	6.2 ± 1.7	5.6 ± 1.8
Empty hole in ground	0.9 ± 0.3	1.1 ± 0.5	1.3 ± 0.3	1.2 ± 0.4	1.1 ± 0.1
% holes in use	89% (466)	60% (124)	57% (138)	81% (285)	72% ± 7.8

(b)	Percentage of trees in 0.25 ha with nest entrances					
	PUM	WAD	WWB	JAM	VOD	Mean %
Base of trees (dbh >5 cm)	90% (174)	91% (92)	95% (80)	93% (227)	86% (129)	91% ± 1.5

Ants used holes in the ground for nesting more than any other type, but they only used 72% of available holes in the ground for nesting. The mean density of *A. gracilipes* nest entrances in supercolonies varied significantly between nest types (Table 1; $F_{3,12} = 4.244$; $p = 0.029$), but not between sites (Table 1; $F_{3,12} = 0.518$, $p = 0.678$). The density of nest entrances was highest at ECR (10.5 nests per m²) and lowest at WAD (2.7 nests per m²). Over 90% (640 of 702) of trees (dbh > 5 cm) observed in 0.25 ha plots had one or more crazy ant nest entrances at their base. Nests were also common inside large fallen and rotting tree trunks, but I did not encounter any within the quadrats in this study. Nests were often found upon felling a dead or dying tree. I uncovered aggregations of workers, pupae and sometimes queens just under leaf litter on the surface of the ground, but it was most likely that these were temporary shelters and not established nest sites because of the unstable nature of the leaf layer.

Ant activity on the forest floor and tree trunks

Foraging by *A. gracilipes* workers was continuous on every available surface 24 hours a day (Figs. 3 and 4). In a 24-hour period at ECR in February 2001, ant activity varied between 13.6 ± 4.3 and 52.2 ± 8.8 ants (mean ± SE) on the card per 30 seconds. There was a suggestion of two peaks of ant activity, one from mid-morning to mid-afternoon (11:30 h and 15:00 h) and one in the middle of the night (22:00 h and 2:00 h). Ant activity was consistently higher at WBT in August than ECR in February; at WBT ant activity varied between 92.3 ± 8.4 and 135.7 ± 3.4 . However, there was no clear pattern in ant activity over the 24-hour period. Dealate queens were observed walking on the forest floor or on tree trunks and roots during the night only at WBT in August (shaded region, Fig. 3).

There was no relationship between diel activity levels on the forest floor and relative humidity at ECR ($F_{1,20} = 0.921$,

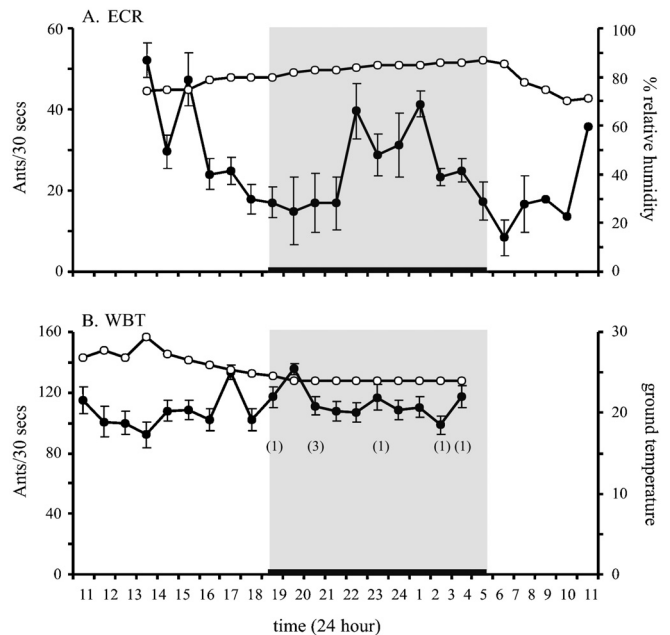


Figure 3. Diel activity of ground foraging workers at (a) ECR, 21–22 February 2001 (24 hours), and (b) WBT, 23–24 August 2001 (18 hours). Each point represents a mean of 20 random counts in a 0.25 ha plot every hour (± SE). (●): ant activity; (○): A. %RH, B. ground temperature (°C). The heavy black bar on the x-axis and the shaded area represents nighttime. Numbers in parentheses indicate the number of dealate queens observed walking in the open in 5-minute searches each hour

$r^2 = 0.044$, $p = 0.349$), or between ant activity on the forest floor and air temperature at ground level at WBT ($F_{1,17} = 3.890$, $r^2 = 0.186$, $p = 0.065$). However, during and immediately after moderate to heavy rains ant activity was noticeably reduced. Ants streamed down tree trunks toward the ground in response to the onset of heavy rain.

Foraging yellow crazy ants were continuously active on tree trunks, in single or multiple trails on larger trees, and haphazardly on all understory vegetation, but consistent with ant

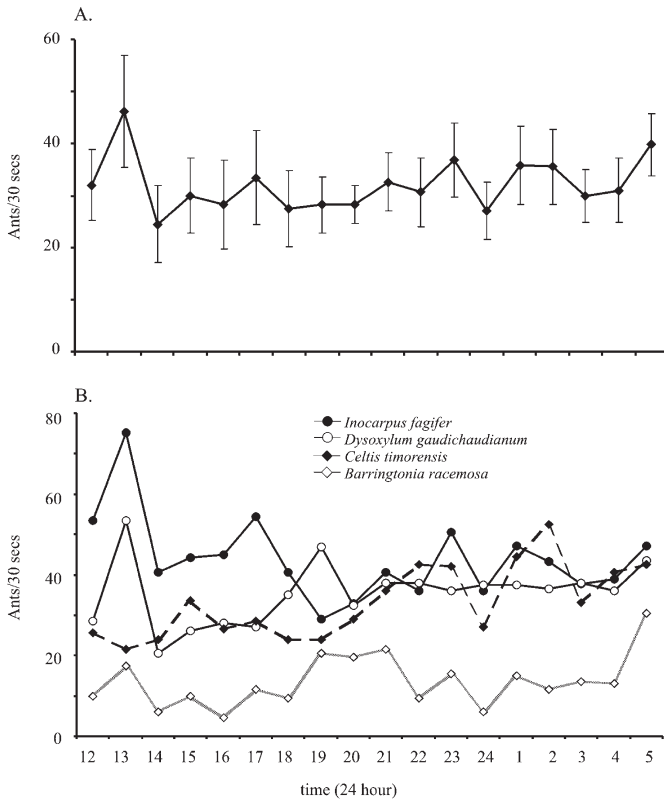


Figure 4. Activity of trunk foraging workers at WBT, 23–24 August 2001 (18 hours). (A.) all tree species combined, where each point represents a mean activity from 11 individual trees (\pm SE), and (B.) species separated. *Inocarpus fagifer*, *Dysoxylum gaudichaudianum*, *Celtis timorensis* and *Barringtonia racemosa*. Error bars omitted on graph B. for clarity

Table 2. Mean intraspecific aggression scores from within isolated nests and supercolonies, between isolated nests and supercolonies, and between supercolonies. Numbers in parentheses represent the distance between the two collection sites (km). Asterisk indicates that the two collection points are located within the same supercolony. IN = isolated nest

	IN 1	IN 2	WAD	SH	WCR	WBT	VOD
IN 2	2.4 \pm 0.2 (7.4)	1.0 \pm 0.0 (0.0)					
SH			1.5 \pm 0.1 (11.3)				
WCR					1.0 \pm 0.2 (0.0*)		
WBT					2.4 \pm 0.3 (1.0)	0.8 \pm 0.4 (0.0*)	
WWB	1.5 \pm 0.2 (7.0)						
HV			0.8 \pm 0.2 (7.3)	0.5 \pm 0.2 (8.1)			
VOD		1.2 \pm 0.1 (5.5)			3.3 \pm 0.3 (1.8*)	2.4 \pm 0.4 (0.8)	1.1 \pm 0.1 (0.0*)

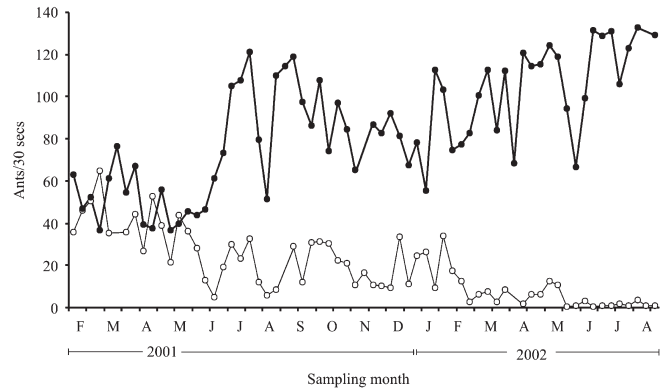


Figure 5. Seasonal activity of ground foraging workers at ECR (●) and WAD (○). Each point on the line is the mean of 20 ant activity counts made weekly in a 0.25 ha plot. Error bars omitted for clarity

activity on the forest floor, there was no apparent diel pattern (Fig. 4A). Ant activity on trunks of *Inocarpus fagifer* was sometimes higher than other species, varying between 29.0 ± 9.3 and 75.3 ± 18.8 ants (mean \pm SE) across a 10 cm \times 10 cm section of the trunk, whereas activity was lower on *Barringtonia racemosa*, varying between 4.5 ± 0.5 and 30.5 ± 7.5 ants across a 10 cm \times 10 cm section of the trunk (Fig. 4B).

Activity of *A. gracilipes* on the forest floor at the older site (approx. 5 yrs old) and new site (<1.5 yrs old) showed distinctively different patterns over a 19-month period. No seasonal pattern in activity occurred at either site. Initial ant activity levels were similar between sites, but diverged after 4–5 months of observation. Activity at the new site increased from approximately 45 ants per 30 secs to >120 ants/30 secs whereas at this point activity at the old site dropped markedly and maintained levels of activity below what constituted a supercolony for the remainder of the observation period (15 months; Fig. 5). Red crabs began to re-establish in the area in early 2002. Ant activity at ECR continued to increase until monitoring ceased in August 2002. Between February 2001 and July 2001, there was no significant relationship between weekly ant activity counts and relative humidity at either the new site ($F_{1,21} = 0.173$, $r^2 = 0.009$, $p = 0.683$) or the old site ($F_{1,20} = 0.047$, $r^2 = 0.003$, $p = 0.831$).

Intraspecific aggression

Aggression between conspecifics of *A. gracilipes* was not apparent in the field, and in aggression levels in laboratory assays were low in the majority of observations. Even ants from isolated nests did not display any form of intraspecific aggression.

Aggression level 1 occurred the most frequently in a total of 136 pair-wise interactions between individual workers. However, I observed 21 aggressive interactions (level 3 and above) between individual workers, and of these eight (6%) involved prolonged fighting. Nevertheless, when these scores were averaged for the nest/supercolony combination, only one

pairing showed a mean aggression level of above three (VOD vs WCR; Table 1). Furthermore, the ants involved in this aggressive interaction were part of the same larger supercolony and located approximately 1.8 km apart. There was a significant relationship between the individual pair-wise level of aggression and the distance of the nests or supercolonies the ants were drawn from ($F_{1,100} = 32.905$, $r^2 = 0.248$, $p < 0.001$); however, it was not in the expected direction. The relationship suggested that the closer the ants were to one another, the more aggressive they were in 10-minute aggression bioassays.

Discussion

The densities of ground foraging *Anoplolepis gracilipes* workers in supercolonies on Christmas Island (>20 million ants per ha) are, to my knowledge, the highest of any ant species recorded (but see Brian, 1965; Higashi and Yamauchi, 1979; Higashi, 1983; Espadaler et al., 2004 for high density populations). These densities were sustained on the ground in individual supercolonies of over 500 hectares, 24 hours a day, 365 days a year and this level of activity was sustained in some instances for up to 6 years (P.T. Green and D.J. O'Dowd, pers. comm.). I have documented that these extreme densities can also rapidly decline, to a point where red crabs can move back into a site without threat of elimination (e.g. WAD).

Foraging worker ants swarmed over everything that entered a supercolony, including crabs, birds and people. Given that in September 2002 supercolonies covered 2378 hectares of Christmas Island rainforest (Green et al., 2004), the total mean biomass of crazy ants on the forest floor in supercolonies at that time could possibly have reached over 1600 kg (>16 tonnes). Queens and brood remained in nests in the ground, and vast numbers of foragers trailed into the rainforest canopy, and were not included in the estimates. As a result, the density and biomass presented here represent a massive underestimate of the total population.

In the Seychelles, estimates based on maximum forager abundance, nest densities, quadrats and subjective assessments yielded predictions of *A. gracilipes* populations (excluding brood) of 5 million ants per ha in areas of high nest density and up to 10 million ants per ha in areas of maximum abundance (Haines and Haines, 1978a). This prediction was also probably an underestimate as no account was taken of foragers and nests in vegetation. Nonetheless, the estimates were based on maximum numbers of foragers and ants in nests (upper 95% limits), unlike this study, where I used means to estimate ant densities. Based on maximum forager activity, the density of foraging *A. gracilipes* workers on the forest floor alone could reach over 70 million ants per ha on Christmas Island.

This rapid field activity assessment has not been used previously in invasive ant studies. However, it was considered appropriate due to the extreme densities and the fact that workers rarely, if ever, formed trails in supercolonies. It would be inappropriate to use this method in estimating the

activity or density of ants where foraging ants would be aggregated, for example in trails (e.g. Argentine ants), or that forage underground (e.g. *Lasius flavus*; Odum and Pontin, 1961; Boomsma and Van Loon, 1982).

Numerical advantages have allowed *A. gracilipes* to dominate the Christmas Island ecosystem. Three hypotheses have been proposed as an explanation for the disproportionate abundance of invasive ants in their introduced range. First, the enemy release hypothesis predicts that escape from coevolved natural enemies and competitors may help [organisms] achieve large colony sizes and increased colony densities as a consequence (Buren, 1983; Williamson, 1996; Crawley, 1997). Second, reduced intraspecific aggression and subsequent allocation of energy and workers to tasks other than colony defence may assist in the maintenance of unicolonial populations and formation of spatially expansive supercolonies (Holway et al., 1998; Tsutsui et al., 2000). Third, the increased efficiency compared to native species, with which invasive ants exploit plant and hemipteran exudates, might fuel high tempo foraging and subsequently increase abundance (Tobin, 1994; Davidson, 1997, 1998; Holway et al., 2002). These three mechanisms operate simultaneously in generating the abundance of *A. gracilipes* on Christmas Island.

Intraspecific aggression was virtually non-existent in the field and very low in laboratory assays within and between supercolonies on Christmas Island. The only aggressive pairwise interaction was between ants belonging to the same supercolony, albeit 1.8 km apart. Although research has shown that diet, nesting material and genetics can influence nestmate recognition (Liang and Silverman, 2000; Tsutsui et al., 2000; Liang et al., 2001; Giraud et al., 2002), I was unable to separate the influence of these factors on aggression levels, but within large supercolonies there is most likely variation in all three that produced aggression.

At supercolony densities on Christmas Island, *A. gracilipes* have two major immediate and obvious impacts, both of which can be viewed as resource exploitation: the acquisition of protein from the red land crab, *Gecarcoidea natalis*, and the promotion of scale insect populations on vegetation within supercolonies from which they acquire carbohydrate-rich honeydew (O'Dowd et al., 2003). Rainforest on the island supports a mean biomass of red land crabs, *Gecarcoidea natalis*, of 114 g per m² (wet mass) (Green, 1997). Even at an average density of 1550 ants per m², *A. gracilipes* kills and eliminates red crabs from the rainforest. Therefore, 1.28 g per m² of *A. gracilipes* workers can overcome and kill approximately 114 g per m² crabs on Christmas Island, over 100 times their own biomass. Despite the pulse of protein at particular times, for example during their annual migration to the ocean for spawning (Hicks, 1985), in the Seychelles high densities of *A. gracilipes* occur in the absence of land crabs or alternative abundant proteinaceous food source, and on Christmas Island supercolonies of *A. gracilipes* persist for years in the absence of land crabs and during times of low invertebrate abundance (Green et al., 1999).

Continuous activity of foraging workers with expanded and translucent gasters on all trunks of both understorey and canopy trees indicate continual sequestering of carbo-

hydrates from honeydew-producing scale insects in the canopy, where densities of adults lac scale insects (Kerriidae) reach over 500 adult females per m twig (Abbott, 2004) and constitute a stable carbohydrate source, as opposed to an unpredictable protein source like insect prey (Sundström, 1993). Access to this abundant carbohydrate-rich food resource may help maintain the high foraging tempo of *A. gracilipes* in supercolonies, and the further monopolisation of resources (Davidson, 1997, 1998). The utilisation of hemipteran honeydew has been implicated in the success of other invasive ant species (Helms and Vinson, 2002, 2003) and the diversification and amplification of impacts caused by *A. gracilipes* on Christmas Island (O'Dowd et al., 2003).

Several invasive ant species have recently been shown to span a continuum of densities in spatially expansive and interconnected supercolonies (Hoffmann et al., 1999; Holway and Case, 2001; Giraud et al., 2002; Helms and Vinson, 2003; Abbott, 2004; Heller, 2004). It is now of critical importance that invasion biologists make the distinction between low-density and high-density supercolonies, especially in relation to their competitive, interference and exploitative capabilities. Numerical advantages increase these capabilities, and frequently facilitate ecological dominance (Haines and Haines, 1978b; Human and Gordon, 1996; Hoffmann et al., 1999; Holway, 1999; Holway and Case, 2001; O'Dowd et al., 2003). Examining the flux in these behaviours across a range of forager densities and nest densities will aid efforts in determining the relative importance of factors contributing to the rapid increase in abundance of invasive ants.

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References

- Abbott, K.L., 2004. *Alien ant invasion on Christmas Island, Indian Ocean: the role of ant-scale associations in the dynamics of supercolonies of the yellow crazy ant, Anoplolepis gracilipes*. PhD Thesis, Biological Sciences. Monash University, Melbourne. 227 pp.
- Barrie, J., 1967. The geology of Christmas Island. *Bureau of Mineral Resources of Australia Record 1967/37*: 46 pp. (unpublished).
- Boomsma, J.J. and A.J. Van Loon, 1982. Structure and diversity of ant communities in successive coastal dune valleys. *J. Anim. Ecol.* 51: 957–974.
- Brian, M.V., 1965. *Social Insect Populations*. Academic Press, London. 135 pp.
- Buren, W.F., 1983. Artificial faunal replacement for imported fire ant control. *Florida Entomol.* 66: 93–100.
- Crawley, M.J., Ed. 1997. *Plant Ecology*. Blackwell Scientific, 736 pp.
- Davidson, D.W., 1997. The role of resource imbalances in the evolutionary ecology of tropical arboreal ants. *Biol. J. Linn. Soc.* 61: 153–181.
- Davidson, D.W., 1998. Resource discovery versus resource domination in ants: a functional mechanism for breaking the trade-off. *Ecol. Entomol.* 23: 484–490.
- Erickson, J.M., 1971. The displacement of native ant species by the introduced Argentine ant *Iridomyrmex humilis* Mayr. *Psyche* 78: 257–266.
- Espadaler, X., S. Rey and V. Bernal, 2004. Queen number in a supercolony of the invasive garden ant, *Lasius neglectus*. *Insect. Soc.* 51: 232–238.
- Falkland, A., 1986. Christmas Island (Indian Ocean) water resources – study in relation to a proposed development at Waterfall. Hydrology and Water Resources Unit, Water Supply, Sewerage and Stormwater Branch of the Transport and Works Division for the Department of Territories. Canberra, Australia.
- Giraud, T., J.S. Pedersen and L. Keller, 2002. Evolution of supercolonies: The Argentine ants of Southern Europe. *Proc. Natl. Acad. Sci. USA* 99: 6075–6079.
- Green, P.T., 1997. Red crabs in rain forest on Christmas Island, Indian Ocean – Activity patterns, density and biomass. *J. Trop. Ecol.* 13: 17–38.
- Green, P.T., S. Comport and D. Slip, 2004. The Management and Control of the Invasive Alien Crazy Ant (*Anoplolepis gracilipes*) on Christmas Island, Indian Ocean: The Aerial Baiting Campaign September 2002. *Unpublished final report to Environment Australia and the Crazy Ant Steering Committee*, Monash University. 79 pp.
- Green, P.T., P.S. Lake and D.J. O'Dowd, 1999. Monopolisation of litter processing by a dominant land crab on a tropical oceanic island. *Oecologia* 119: 435–444.
- Haines, I.H. and J.B. Haines, 1978a. Colony structure, seasonality and food requirements of the crazy ant, *Anoplolepis longipes* (Jerd.), in the Seychelles. *Ecol. Entomol.* 3: 109–118.
- Haines, I.H. and J.B. Haines, 1978b. Pest status of the crazy ant, *Anoplolepis longipes* (Jerdon) (Hymenoptera: Formicidae), in the Seychelles. *Bull. Entomol. Res.* 68: 627–638.
- Heller, N.E., 2004. Colony structure in introduced and native populations of the invasive Argentine ant, *Linepithema humile*. *Insect. Soc.* 51: 378–386.
- Helms, K.R. and S.B. Vinson, 2002. Widespread association of the invasive ant *Solenopsis invicta* with an invasive mealybug. *Ecology* 83: 2425–2438.
- Helms, K.R. and S.B. Vinson, 2003. Apparent facilitation of an invasive mealybug by an invasive ant. *Insect. Soc.* 50: 403–404.
- Hicks, J., 1985. The breeding behaviour and migrations of the terrestrial crab *Gecarcoidea natalis* (Decapoda: Brachyura). *Aust. J. Zool.* 33: 127–142.
- Higashi, S., 1983. Polygyny and nuptial flight of *Formica (Formica) yessensis* Forel at Ishikari Coast, Hokkaido, Japan. *Insect. Soc.* 30: 287–297.
- Higashi, S. and K. Yamauchi, 1979. Influence of a supercolonial ant *Formica (Formica) yessensis* Forel on the distribution of other ants in Ishikari Coast. *Jap. J. Ecol.* 29: 257–264.
- Hoffmann, B.D., A.N. Andersen and G.J.E. Hill, 1999. Impact of an introduced ant on native rain forest invertebrates: *Pheidole megacephala* in monsoonal Australia. *Oecologia* 120: 595–604.
- Hölldobler, B. and E.O. Wilson, 1990. *The Ants*. Belknap Press, Cambridge, Mass. 732 pp.
- Holway, D.A., 1998. Effect of Argentine ant invasions on ground-dwelling arthropods in Northern Californian riparian woodlands. *Oecologia* 116: 252–258.
- Holway, D.A., 1999. Competitive mechanisms underlying the displacement of native ants by the invasive Argentine ant. *Ecology* 80: 238–251.
- Holway, D.A. and T.J. Case, 2001. Effects of colony-level variation on competitive ability in the invasive Argentine ant. *Anim. Behav.* 61: 1181–1192.
- Holway, D.A., A.V. Suarez and T.J. Case, 1998. Loss of intraspecific aggression in the success of a widespread invasive social insect. *Science* 282: 949–952.

- Holway, D., L. Lach, A.V. Suarez, N.D. Tsutsui and T.J. Case, 2002. The causes and consequences of ant invasions. *Ann. Rev. Ecol. Syst.* 33: 181–233.
- Human, K.G. and D.M. Gordon, 1996. Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. *Oecologia* 105: 405–412.
- Liang, D., G.J. Blomquist and J. Silverman, 2001. Hydrocarbon-released nestmate aggression in the Argentine ant, *Linepithema humile*, following encounters with insect prey. *Compar. Biochem. Phys. B* 129: 871–882.
- Liang, D. and J. Silverman, 2000. “You are what you eat”: Diet modifies cuticular hydrocarbons and nestmate recognition in the Argentine ant, *Linepithema humile*. *Naturwissenschaften* 87: 412–416.
- Mitchell, B.A., 1985. A vegetation survey of Christmas Island. Australian Nature Conservation Agency. Canberra, A.C.T., Australia.
- O’Dowd, D.J., P.T. Green and P.S. Lake, 1999. Status, impact and recommendations for research and management of exotic invasive ants in Christmas Island National Park. *Report to Environment Australia*, Monash University. Melbourne. 60 pp.
- O’Dowd, D.J., P.T. Green and P.S. Lake, 2003. Invasional ‘meltdown’ on an oceanic island. *Ecol. Lett.* 6: 812–817.
- Odum, E.P. and A.J. Pontin, 1961. Population density of the underground ant, *Lasius flavus*, as determined by tagging with P32. *Ecology* 42: 186–188.
- Porter, S.D. and D.A. Savignano, 1990. Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. *Ecology* 71: 2095–2106.
- Sundström, L., 1993. Foraging responses of *Formica truncorum* (Hymenoptera:Formicidae); exploiting stable vs spatially and temporally variable resources. *Insect. Soc.* 40: 147–161.
- Tobin, J.E., 1994. Ants as primary consumers: diet and abundance in the Formicidae. In: *Nourishment and Evolution in Insect Societies* (J.H. Hunt and C.A. Nalepa, Eds). Boulder, Westview Press: 279–308.
- Tsutsui, N.D., A.V. Suarez, D.A. Holway and T.J. Case, 2000. Reduced genetic variation and the success of an invasive species. *Proc. Natl. Acad. Sci. USA* 97: 5948–5953.
- Williamson, M., 1996. *Biological Invasions*. Chapman & Hall, London. 244 pp.



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