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Limiting spread of a unicolonial invasive insect and characterization of seasonal patterns of range expansion

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Abstract

Limiting dispersal is a fundamental strategy in the control of invasive species, and in certain situations containment of incipient populations may be an important management technique. To test the feasibility of slowing the rapid spread of two Argentine ant (*Linepithema humile*) supercolonies in Haleakala National Park, Hawaii, we applied ant bait and toxicant within an experimental plot situated along a supercolony boundary. The 120 × 260 m plot simulated a small section of what could potentially be a 120 m wide treatment encompassing the entire expanding boundaries of both supercolonies. Foraging ant numbers at baited monitoring stations decreased sharply within two weeks after treatment, and ant spread was completely halted within the plot for at least one year. In contrast, an adjacent untreated colony boundary advanced an average of 65.2 m over the course of 1 year. Most of this spread took place in the summer and fall, at the time of highest ant abundance at bait monitoring stations, while no outward dispersal occurred during the spring and early summer. These patterns are consistent with the hypothesis that local budding dispersal in this unicolonial species stems from density dependent pressure rather than inherent founding behavior associated with mating. Based on results from this experiment, we are investigating the effectiveness of annual boundary treatments in slowing the Argentine ant invasion at Haleakala National Park. The goals of this program are to protect populations of native arthropods and to keep options open for eventual attempts at eradication.

Introduction

The process of dispersal is a key feature in the success of most invasive species. A species' ability to direct propagules to favorable new habitat is a prerequisite for attaining widespread ecological dominance. Conversely, the prevention of dispersal is an important management technique for limiting the success of invasive species. It is widely recognized that quarantine procedures aimed at preventing human-mediated dispersal of biotic organisms to new geographic regions are a critical step in slowing the current worldwide flood of biological invasions. At the same time, it is often assumed that once an invasive species gains a foothold in a new region, preventing its local spread is nearly impossible, or at least logistically and economically unrealistic. Despite this common perception, land managers have successfully employed various barriers or other techniques to exclude destructive non-native species from natural areas, including ungulate-proof fences and snail barriers in Hawaii (Stone and Loope 1996; Stone 1999), small mammal trapping and baiting on a number of Pacific islands (Robertson et al. 1994; Gillies and Pierce 1999; Hodges and Nagata 2001; Vander Werf and Smith 2002) and snake-proof fences on Guam (Campbell 1999). This approach has typically been used to protect, often indefinitely, rare endemic populations, species, or even whole ecosystems when the invasive species of concern is widespread and eradication is not a possibility in the foreseeable future.

In cases of relatively early detection, however, prevention of local spread of an invasive species may serve the dual purposes of protecting native resources as well as preserving future options for eradication by not allowing the invader to become overly widespread in the first place. By buying time, this latter technique of containment could in some situations be a critical step in the management and eventual eradication of an invasive species.

Ants are notorious invaders in both continental and insular ecosystems. Several dozen ant species frequently disperse with the help of human activities, and are often referred to as tramp ants (Holldobler and Wilson 1990; Passera 1994). While many of these species remain associated with human presence, others are known to spread to natural areas where they can displace native species (Porter and Savignano 1990; Human and Gordon 1996; Hoffman et al. 1999), cause indirect impacts (Suarez and Case 2002) and even disrupt ecosystem processes (Christian 2001). The most invasive of these tramp species typically share a number of characteristics that may facilitate their success as invaders, but at the same time may make them more vulnerable to management. These characteristics include multiple queens per nest as well as little or no intraspecific aggression among many interconnected nests within a continuously occupied area (Passera 1994; Holway et al. 2002). This condition is termed unicoloniality, and the spatially contiguous territories occupied by these species are often referred to as 'supercolonies' to indicate the co-operative behavior that occurs throughout. Unicoloniality often, but not always, coincides with a mode of local dispersal known as budding, in which queens do not participate in a nuptial flight, but instead move short distances across the ground surface to new nest locations with a retinue of worker ants. The result is a gradual expansion of the entire supercolony, which is much less dramatic than the long-distance jump dispersal mediated by humans (Holway 1998; Suarez et al. 2001), but which is nevertheless important in the local ecological dominance of these species. Consequently, prevention of budding dispersal may, under specific circumstances, be an important and effective management technique for invasive ants.

The Argentine ant, *Linepithema humile* (Mayr), is one of the most successful of all invasive ant species. Native to South America, it is now established at many locations on six continents and a number of oceanic islands (Suarez et al. 2001). In the Hawaiian Islands, its tolerance for cooler climates has allowed it to spread into high elevation sites upslope from colonies of the other highly invasive ants that are dominant at low to middle elevations. It occurs up to elevations of 2640 m on the island of Hawaii (Wetterer et al. 1998), and in Haleakala National Park on Maui we currently find it up to elevations of 2850 m. The subalpine shrubland and aeolian zones found at this elevation in Haleakala National Park are still largely intact, supporting native plant communities as well as a diverse arthropod fauna with a high rate of local endemism (Beardsley 1980). Because Hawaiian arthropods evolved in the absence of ants (Wilson and Taylor 1967), many are highly vulnerable to ant predation and competition (Perkins 1913; Gillespie and Reimer 1993; Reimer 1994). Cole et al. (1992), for instance, found that the Argentine ant significantly impacts a wide range of native arthropod species, including essential pollinators, in Haleakala National Park. It is now considered to be the single greatest threat to the survival of a number of unique taxa endemic to upper Haleakala volcano.

Since the Argentine ant was first recorded in Haleakala National Park in 1967 (Huddleston and Fluker 1968), it has expanded its territory to occupy two separate supercolonies with a combined area of over 500 ha. Unfortunately, concerted efforts to contain or eradicate the ant were not initiated until the mid 1990s, at which point the only realistic strategy involved baits and toxicants. Our most promising results were obtained with the commercial product Maxforce Granular Ant Bait, a protein bait formulated with the toxicant hydramethylnon (Krushelnycky and Reimer 1998b). While eradication was not achieved in any test plots, Maxforce consistently reduced the number of foraging ants by over 90%. We hypothesized that this reduction might suppress normal colony activities, including budding dispersal, for some period of time.

With the two supercolony boundaries rapidly advancing (at rates of ≈25–150 m/year, unpubl. data) and no method for eradication yet available, we decided to test whether treatment of expanding supercolony margins with Maxforce Granular Ant Bait would halt spread. We regard the use of pesticide in a natural area as a last resort, in this case justified by the consequences of non-action. In addition, the toxicant hydramethylnon has a number of characteristics that minimize adverse effects. It has low acute toxicity towards birds and mammals (EPA 1998), is not taken

up by plants (Bacey 2000), is practically insoluble in water, does not leach from soil (EPA 1998), and it degrades very rapidly through photolysis (aqueous photolysis half-life is <1–3.5 h (Mallipudi et al. 1986; Chakraborty et al. 1993); soil photolysis is biphasic with first half-life at 4 days and second at 30 days (EPA 1998); daylight photolysis half-life is roughly 12 h when formulated in Amdro bait granules (Vander Meer et al. 1982)). When formulated in bait granules and broadcast in a pasture subject to foraging by Red Imported Fire Ants (*Solenopsis invicta* Buren), it was undetectable in soil cores within 24–48 h (Apperson et al. 1984).

The greatest non-target effects from Maxforce treatment at Haleakala are therefore likely to be on other arthropods. While hydramethylnon is non-toxic by cuticular contact (EPA 1998), some arthropod groups, potentially including predators and a variety of decomposers, are likely to ingest the bait. We feel this risk to arthropods is acceptable because of the highly detrimental effects of the Argentine ant on these same groups of arthropods. Unlike impacts caused by the Argentine ant, non-target impacts resulting from the use of hydramethylnon will be relatively localized and reversible. Most importantly, while the ant has currently colonized ~5% of the park, we estimate that it has the potential to invade nearly 50%, including over 75% of the park's subalpine shrubland and aeolian habitats, based on its historic pattern of spread and apparent temperature and moisture tolerances (unpubl. data). While the Argentine ant occurs in some other parts of the island, ant surveys suggest that the two supercolonies in Haleakala National Park are well isolated from these areas. Future spread up to the park via overland budding seems unlikely because of unsuitable intervening habitat, and due to raised awareness among park employees, we believe that additional human-mediated introductions to the park can be prevented or quickly detected. We therefore feel that this situation represents a good candidate for temporary containment efforts, allowing us to keep options open for future eradication (using a more effective bait–toxicant combination) and helping to preserve biodiversity in the park. Seasonal variation in the ant's natural dispersal behavior might affect the success of a containment program. Our goals in this study, therefore, were to determine the effectiveness of treatment of a supercolony boundary in limiting spread, and to concurrently learn more about the seasonal patterns of budding dispersal of the Argentine ant in an adjacent untreated area.

Materials and methods

Under ideal conditions, multiple randomized treatment and control plots would be employed to test the effectiveness of a bait and toxicant treatment in limiting ant spread at Haleakala National Park, Hawaii. Because we were concerned about unnecessarily overusing pesticide before the efficacy of this technique was known, as well as considerations of cost and feasibility, we instead chose to test a single treatment plot in relation to a single adjacent control area. While this limits our ability to extend inferences to the entire boundaries of both supercolonies, we recognized beforehand that future variation in the success of this technique was likely over both space and time, regardless of how many test plots we initially employed. Any subsequent extension of treatment to the entire boundaries of both supercolonies would still be considered 'experimental', and we judged that it was sufficient at the time to know the effectiveness of a treatment in a single, well-chosen plot.

We established a 2.9 ha plot along the boundary of the lower Argentine ant supercolony at ca. 2250 m elevation (Figure 1). The dimensions of this plot, 260 m long by 120 m wide, were chosen to test the efficacy of a relatively narrow border treatment. We randomly placed the plot along a rapidly expanding section of the ant boundary, and positioned the roughly rectangular plot so that the ant-occupied portion was only 100 m wide by 260 m long (Figure 1). A 20 m 'margin of safety' therefore extended beyond the known supercolony boundary to accommodate short-term movement and small errors in boundary mapping. This plot was meant to simulate a small section of what could potentially be a 120 m wide treatment encompassing the entire expanding margins of both supercolonies.

For the purpose of monitoring, we placed four transects in the treated plot and four transects in the adjacent untreated shrubland that served as the control area (Figure 1). A control 'plot' was unnecessary, as all monitoring took place on the transects. The closest control transect was located ~40–50 m from the border of the treated plot (Figure 1). In both the treated plot and the control area, the four parallel transects were spaced 20 m apart, and on each transect, bait monitoring stations were marked every 10 m, starting with station 1 located 100 m behind the ant boundary and ending with station 13 located 20 m beyond the boundary. As the ant boundary expanded outward from its original location at station 11 (on all 8 transects) and

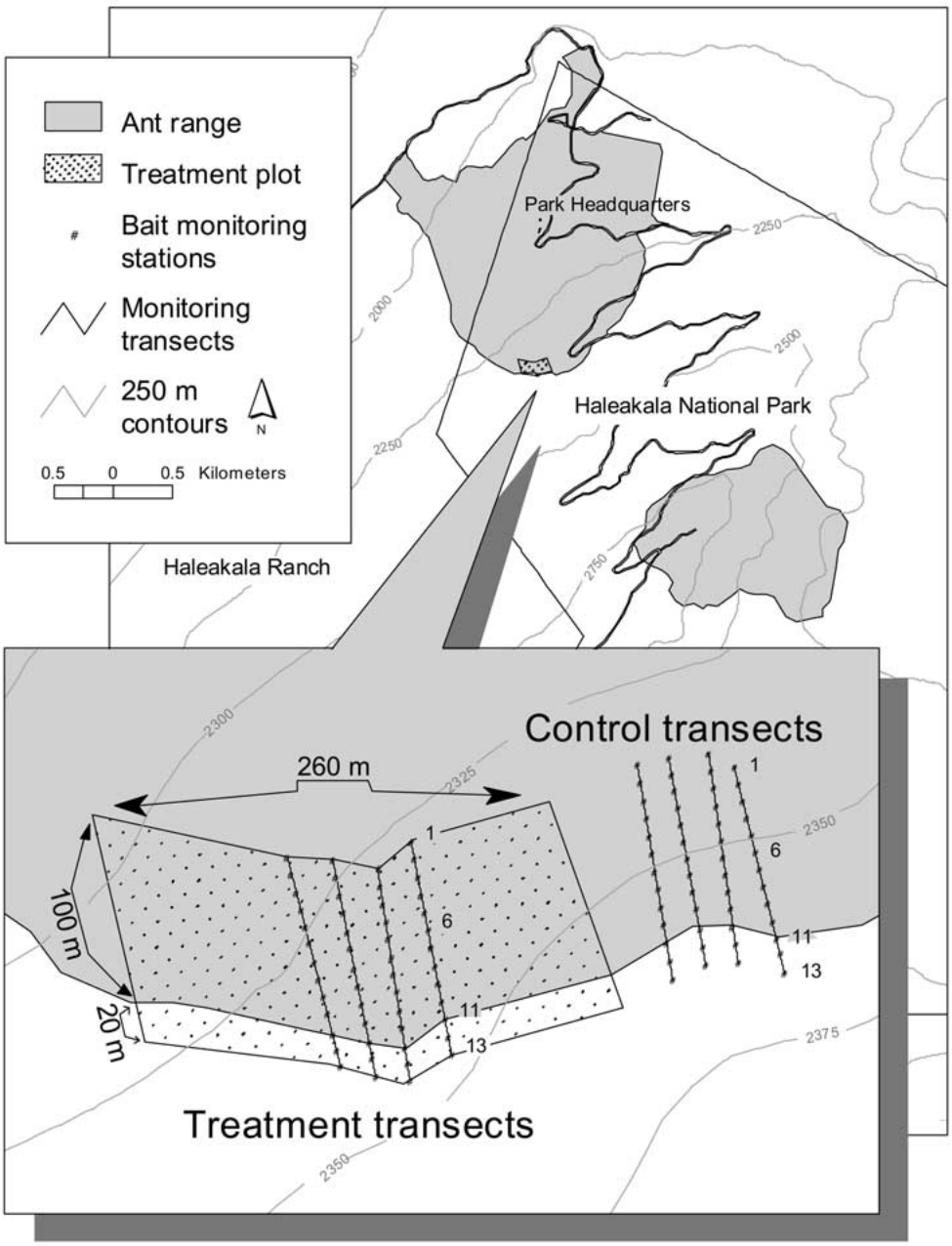


Figure 1. Location of the two Argentine ant supercolonies and experimental treatment plot in Haleakala National Park. The inset is a closer view of the study area, showing the dimensions of the treatment plot and locations of the treatment and control monitoring transects.

moved beyond station 13, we added new stations every 10 m as needed. To minimize the chances of lateral recolonization from the plot's side borders influencing post-treatment monitoring on the transects, we placed the four treated transects in the center of the plot with a 100 m treated buffer on either side (Figure 1).

Maxforce Granular Ant Bait (a.i. 0.9% hydramethylnon, Clorox Corp.) was aerially broadcast in the plot at an application rate of 2.25 kg/ha (2 lbs/acre) on August 19, 1996. We chose this application rate because our prior experimental results with Maxforce bait in the park were obtained using 2.25 kg/ha

(Krushelnycky and Reimer 1998b). A bait hopper, built specifically for controlling big-headed ants, *Pheidole megacephala* (F.), in pineapple fields, was suspended from a helicopter and flown over the plot. We treated on the morning of a warm, dry day to ensure maximum initial ant foraging and retrieval of bait.

Monitoring consisted of a monthly assessment of both relative ant numbers and distance of boundary movement from August 1996 to 1997. Relative ant numbers were measured in the first few days of each month using bait cards. We used a 9 : 1 mixture of corn syrup and blended fermented fish (sigamid), placed on a 7.6 × 6.3 cm (3 × 2.5 inch) index card. At each bait monitoring station, we placed three bait cards on the ground at least 2 m apart, for an initial total of 132 bait cards in both the treated and control areas. This number increased as transects were lengthened. After 45 min, we counted the total number of ants on each card. Numbers of ants counted on the three bait cards at each monitoring station were pooled as a single data point. In an effort to control for variable weather conditions, we did not conduct monitoring on rainy or excessively windy days. We compared ant counts between treated and control transects, as well as between points in time of interest on the treated transects, with a one-way ANOVA followed by the Tukey Honestly Significant Difference (HSD) test on the rank-transformed data, because count data were not normally distributed. We measured distance of boundary movement at the beginning of each month by searching on the ground, under rocks and on vegetation on each of the eight transects for the furthest presence of ants beyond the previously determined ant boundary.

Spatial patterns of regrowth in the monitored area of the plot and recolonization from the rear of the plot were analyzed using the percent recovery at 11.5 months post-treatment at each monitoring station as a data point. We excluded stations for which pre-treatment ant counts averaged fewer than five ants per bait card from this analysis, as we judged that bait station monitoring is inadequate for accurately measuring relative ant densities at such low levels. Ant recovery at stations located in the rear of the plot were then compared with stations in the front of the plot with the Wilcoxon Rank Sum test, where rear was defined as station numbers 1–3 on each transect, and front was defined as stations 4 and higher on each transect. We chose this point of division between front and rear because it divided the number of stations included in the analysis roughly in half; most of the stations closer to the ant boundary were excluded according to the criteria stated above.

Rainfall and soil temperature may influence both degree of foraging and rate of ant spread. To address these factors, we obtained soil temperature at 5 cm depth and rainfall data from a climate station (HaleNet I station 151, Giambelluca 2000) and a National Weather Service rainfall gauge (Haleakala Ranger Station, NCDC 1996, 1997) located at Haleakala National Park Headquarters, ~1.25 km from the study site. Average daily soil temperature data from May 1997 through August 1997 were not available. We used Spearman rank correlation to assess relationships between monthly rainfall and monthly distance of spread on control transects, and between mean daily soil temperature on monitoring days and mean number of ants observed at control bait stations. For the former comparison, we used the 11 months of September 1996 through July 1997 for which we had measured distance of spread over the entire month. For the latter comparison, we used only the 9 months of August 1996 through April 1997 for which daily soil temperature data were available. In the few instances where control bait station monitoring was conducted on more than one day, mean daily soil temperatures for all applicable days were averaged. All statistical analyses were performed in JMP IN v. 3.2.6 (SAS Institute 1996).

Results

Ant numbers

The mean number of foraging ants at bait monitoring stations decreased dramatically at two weeks post treatment on the treated transects but not on the control transects (Figure 2). Results of the ANOVA on bait station counts indicated that differences between treated and control areas, as well as differences between monthly counts within each, were highly significant ($F = 48.43$; df = 25, 1329; $P < 0.0001$). According to the Tukey HSD test, ant counts on the treated transects were different from those on the control transects at every point in time except for the pre-treatment monitoring event in August 1996. Within the treated plot, ant count numbers remained low until July and August 1997, peaking at 21.0% of pre-treatment values in July. Only in July and August 1997 did ant counts within the treated plot become significantly higher than counts at 2 weeks post-treatment. Ant numbers at bait

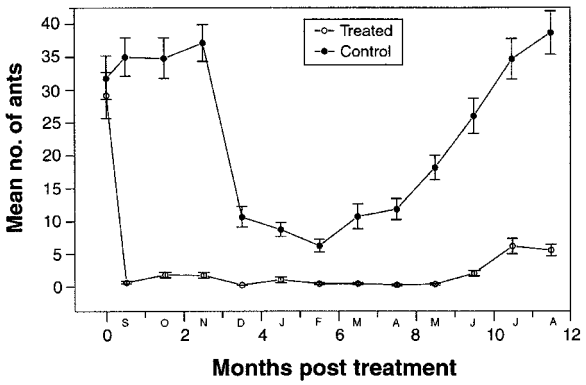


Figure 2. Mean numbers of ants at bait monitoring stations in treated and control areas. Data were averaged among all stations in each area for each date and were collected at the beginning of each month indicated. Error bars indicate ±1 S.E.

monitoring stations on control transects remained high until December, after which large reductions began. These reductions at control stations appear to be related to the ant's seasonal life cycle (Markin 1970b), and foraging numbers at control stations rebounded in the spring and summer of the following year (Figure 2).

Figure 3 illustrates the spatial patterns of foraging ants along the bait station transects, which ran perpendicular to the invasion front, in the treated plot and the adjacent control area. Numbers of ants counted along the four transects in both areas were averaged for each of the bait monitoring stations, showing the mean number of ants every 10 m as one progresses from station 1, located 100 m behind the original supercolony boundary, to station 11, located at the original boundary, and beyond. Ant numbers at bait monitoring stations decrease relatively gradually as the supercolony boundary is approached (Figure 3, pre-treatment data 8/11/96). The density of ants, and possibly also the density of nests, presumably follows this same pattern. By 2 weeks post-treatment (9/2/96), however, this density had dropped dramatically along the entire length of the treated transects. Only the stations located 100 m behind the original front (numbered 1) had a detectable presence of ants. Ant numbers along the control transects were not similarly affected, and advanced to new stations throughout the year.

At 11.5 months post-treatment, percent recovery in the rear of the plot as a whole was not significantly higher than recovery in the front of the plot (see 'Materials and methods' for explanation of 'rear' and 'front') (Wilcoxon Rank Sum test; $S = 194$; $P = 0.213$). Instead, ant numbers recovered more

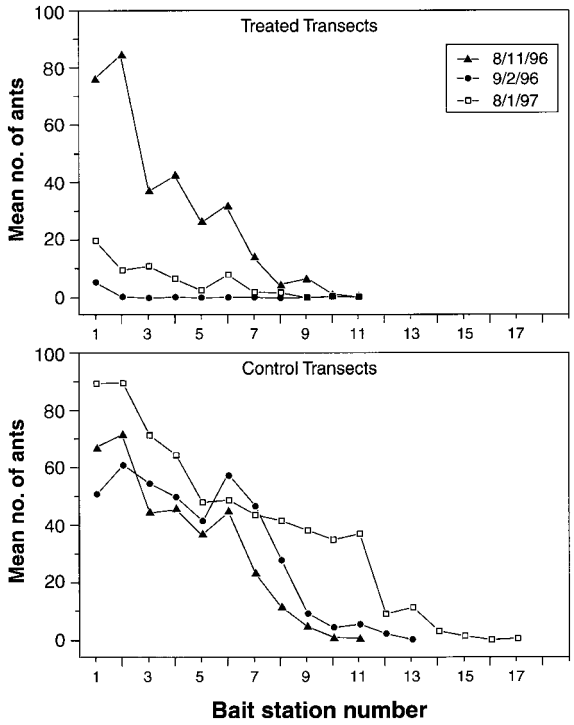


Figure 3. Mean numbers of ants along treated and control transects, grouped by bait monitoring station number for dates of interest. Monitoring stations were situated at 10 m intervals along transects perpendicular to the invasion front. On treated transects the invasion front did not advance over the course of the study period, while on control transects the ants advanced from bait station 11 (8/11/96) to beyond station 17 (8/1/97). Error bars were not included in the interest of visual clarity.

substantially on one side of the plot (transects 1 and 2) than the other (transects 3 and 4).

Boundary movement

Figure 4 shows mean monthly distance of boundary movement along the four treated transects and four control transects. No movement occurred along the treated transects, while total boundary movement along the four control transects during the 1-year study period ranged from 62 to 72 m, with a mean of 65.2 m. Monthly movement in the untreated control area was highest in the summer (1996 and 1997) and fall (1996) and lowest in the spring (1997).

Weather conditions and correlations

While a number of monthly rainfall totals departed substantially from normal during the study period,

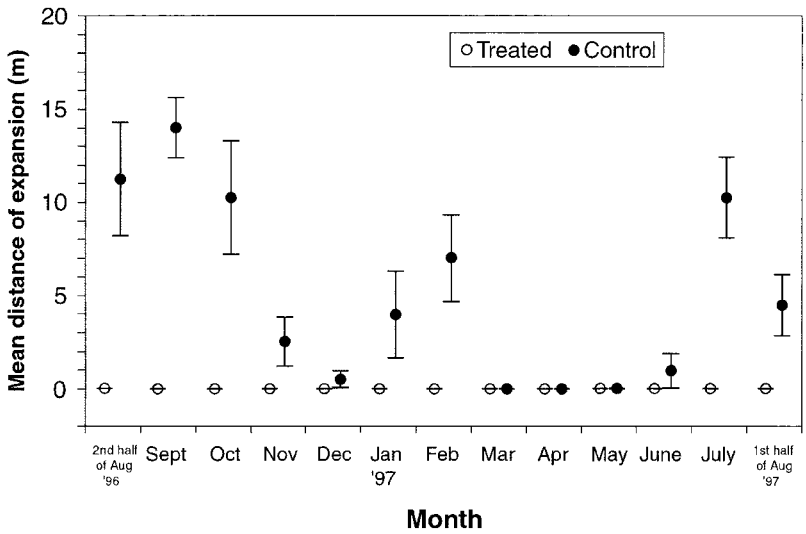


Figure 4. Mean monthly distance of ant boundary expansion on treated and control transects. Values for each month indicate the total distance of spread during that month, with the exception of the first and last values. These represent only half of the month of August in 1996 and 1997, respectively. Error bars indicate ±1 S.E.

the total rainfall for the annual period was only 34% above normal (Table 1). We found that monthly rainfall and distance of movement on the control transects were not strongly correlated ($r_s = -0.276$; $n = 11$; $P = 0.412$). The relationship between mean daily soil temperature at 5 cm depth and numbers of foraging ants at control bait monitoring stations was somewhat stronger, but also not statistically significant at a 95% confidence level ($r_s = 0.510$; $n = 9$; $P = 0.160$).

Discussion

The single aerial application of Maxforce Granular Ant Bait in our 120 m wide supercolony boundary plot appeared to reduce overall numbers of foraging ants at baits within 2 weeks after treatment, and apparently stopped the expansion of ants at the invasion front. Although we only used one treatment plot at this time, we find it extremely unlikely that some factor other than the Maxforce treatment, such as chance, could have produced a pattern wherein ant numbers in treated and control areas were not statistically significantly different prior to treatment but were vastly different immediately after treatment. After all, the toxicant hydramethylnon is designed to kill insects, and the observed pattern of mortality closely matches numerous previous and subsequent efforts with Maxforce Granular Ant Bait at Haleakala National Park.

Table 1. Weather conditions at Haleakala National Park headquarters during the study period.

Month	Rainfall[a]		Mean daily soil temperature (°C)[b]
	Monthly total (mm)	% of normal	
Aug '96	24.1	42.4	19.2
Sep	82.0	174.6	16.0
Oct	9.1	12.3	18.1
Nov	205.2	120.0	11.9
Dec	436.6	240.4	10.3
Jan '97	214.4	81.5	11.9
Feb	151.1	86.7	11.5
Mar	266.7	142.7	10.2
Apr	160.8	103.1	10.9
May	28.2	43.5	n/a
Jun	196.6	634.4	n/a
Jul	229.4	414.2	n/a
Aug '97	38.4	67.4	n/a
Total	2042.7	134.5	—

[a]Obtained from the National Climatic Data Center (NCDC 1996, 1997).

[b]Mean soil temperatures listed (Giambelluca 2000) were measured at a depth of 5 cm and correspond to the days on which bait station monitoring was conducted. Data for May through August 1997 were not available.

The immediate reduction of foraging ants was uniform throughout the monitored region of the plot (Figure 3), and recovery of ant numbers was very modest until 10.5 months post-treatment (Figure 2): maximum recovery in foraging ant numbers throughout the 1-year study period only reached 21% of

pre-treatment levels. Recolonization into the plot from its rear border may have been partially responsible for an increase in ant numbers during the course of the study, but after almost one year, recovery of ant numbers relative to pre-treatment values was not uniformly higher across the rear of the plot *versus* the front of the plot. While foraging workers constitute only a portion of an ant colony, previous studies using Maxforce at Haleakala (e.g. Krushelnycky and Reimer 1998b) strongly suggest that the high mortality recorded in this group represents more uniform results throughout the colony. Despite the fact that some nests clearly survived and began rebuilding, the net reduction in our relatively narrow test plot was sufficient to yield complete containment over the course of one year.

In contrast, the boundary in the adjacent control area advanced, on average, 65.2 m in the same period of time, a rate of spread that falls within the range of other reported rates for this species (reviewed in Suarez et al. 2001). The untreated boundary did not expand evenly throughout the year, however, and the particular life history traits of the Argentine ant likely influence the temporal patterns of this budding dispersal. Mating of newly emerged virgin queens is thought to occur within the natal nest, with the newly mated queens being subsequently assimilated in the nest (Newell and Barber 1913; Markin 1970b; Benois 1973), resulting in the state of polygyny characteristic of this species outside its native range. Dispersal pressure therefore does not appear to stem from inherent behavior by daughter queens to found new nests upon mating, as is the case in monogynous ant species which undergo a nuptial flight (Holldobler and Wilson 1990). Instead, as noted by Benois (1973), dispersal in this species appears to occur when worker production in the colony approaches its peak and total ant abundance is high.

This interpretation is largely supported by the pattern of spread that we observed on the untreated transects at Haleakala during 1996 and 1997 (Figure 4). Most of the supercolony expansion occurred during the months of July through October, and coincided fairly well with the peaks in ant numbers at control bait monitoring stations (Figure 2). Densities of ants within nests may have grown sufficiently high during these months to trigger nest splitting and budding, resulting in a period of range expansion. Consistent with this view, movement slowed during November 1996, just as ant numbers at control bait monitoring stations declined sharply. Without accurate measures of absolute ant abundance, we cannot be certain of seasonal patterns of within- or between-nest densities. Unfortunately, changes in absolute ant abundance over time are difficult to quantify because measurement typically results in disruption or destruction of nests, and non-destructive bait monitoring may be an imperfect proxy. For instance, the seasonal fluctuation of ant numbers at our bait monitoring stations could be alternatively explained in part by a seasonal shift in bait preference, or by seasonal changes in foraging behavior dictated by temperature. Our monitoring bait included both carbohydrate and protein, however, and therefore should have addressed the ant's year-round food requirements and preferences (Markin 1970a; Krushelnycky and Reimer 1998a). The role of temperature is more complicated. We did not find a very strong relationship between soil temperature and monthly foraging ant numbers, although a weak trend is evident and might be clarified with more data. This correlation analysis, however, cannot determine whether foraging ant numbers at bait stations fluctuated throughout the year solely because of fluctuating soil temperature, or whether they fluctuated as a result of changes in absolute ant numbers during the ant's annual life cycle, since absolute numbers in the latter case would also be correlated with temperature through its association with season. Argentine ant foraging at Haleakala is in fact dependent on soil temperature on the scale of daily behavior (Krushelnycky, unpubl. data), however, we believe that larger colony fluctuations are more important on the scale of seasons. In the course of field work we have observed that, roughly speaking, the production of worker brood is high in mid- and late summer, and decreases sharply during the winter. This reduction of brood followed by mortality of aging adult workers should alleviate crowding in the nest in the late fall and winter, and may in large part explain the decreasing rate of colony expansion. In support of this inference, Markin (1970b) found that the proportional abundance of worker pupae in southern California peaked in October, and then decreased dramatically over the winter.

Interestingly, there was virtually no ant spread in the control area from March through June 1997. This is the season during which new queens emerge and mate in Argentine ant colonies in southern California (Markin 1970b). We have observed a similar pattern at Haleakala, with the main production of sexual castes beginning around April and male production continuing into summer and fall. The lack of dispersal

during the spring of 1997 may have been tied to low worker densities, but could potentially also have been a result of temporarily reduced queen numbers: both Markin (1970b) and Keller et al. (1989) found that the production of new queens is preceded by an annual queen execution event in which mated queens are killed by workers. This event may be necessary to reduce inhibition pheromones released by mated queens that suppress, through the control of colony behavior, the development of new larval queens (Keller et al. 1989). Timing of the execution ranged from January and February in southern California to April and May in France, and Keller et al. (1989) documented that up to 90% of the old, mated queens were killed. In the near absence of queens, it seems unlikely that nests would bud and expand into new territory. We collected no data that would document the occurrence of such an event at Haleakala in the spring of 1997; however, this would be a worthwhile subject of research relevant to continuing control efforts.

The ant boundary did advance somewhat in January and February 1997, which is difficult to explain from the perspective of density-dependent dispersal behavior. Both field observations and the bait station data collected here suggest relatively low ant abundance in winter months. It is possible that this movement may represent a lower background level of nest relocation. Argentine ants, like many ant species (Herbers 1985; Holldobler and Wilson 1990), regularly shift their nest sites in response to disturbance, changing abiotic conditions, food resources and other factors (Markin 1970b; Benois 1973; Holway and Case 2000). This type of nest relocation at the supercolony margins may naturally lead to a low level of range expansion. We would need to measure additional annual cycles of ant spread at Haleakala to better understand these results.

By comparison, Sanders et al. (2001) monitored a northern California Argentine ant invasion over a period of seven years. They found that, on average, the ant gained territory from May to September and lost territory from September to May. While it cannot be determined from these data whether Argentine ants in northern California dispersed during the exact months of high dispersal activity at Haleakala, this seasonal pattern roughly matches the one recorded here: the Argentine ant was distributed significantly more broadly in September than in May (Sanders et al. 2001). During the one-year study at Haleakala, however, substantial spread occurred during September and October, and significant loss of territory was not observed.

Timing of our treatment coincided with the early to middle part of the Argentine ant's dispersal phase at Haleakala. We chose to apply the bait and toxicant when worker ant abundance was high to improve the chances of maximum retrieval and distribution of the bait among nests. An alternative approach would entail treating when the colony is at an annual low, requiring less mortality to achieve the same reduction in worker numbers, and targeting the colony before the period of high dispersal. Of primary importance, however, is the reduction of queen numbers rather than worker numbers, and because new queens are produced only once per year (Markin 1970b), annual growth in the ant supercolony as a whole proceeds with no increase in queen number. The worker to queen ratio should therefore be lowest during the winter and spring, which could result in less effective bait retrieval and distribution to queens at this time of year. Instead, we treated as the worker to queen ratio should have been reaching its plateau. This apparently suppressed worker production and budding dispersal throughout the ensuing year, even during the early stages of the subsequent dispersal period.

Management implications

The successful eradication or control of invasive ants is notoriously difficult. The 40-plus year campaign to control the Red Imported Fire Ant (*S. invicta*) in the southeast US is the most infamous case in point (Williams 1994). In addition to the inherent difficulties of eradicating social insects (e.g. Abedrabbo 1994; Beggs et al. 1998; Krushelnycky and Reimer 1998b), the effort involving *S. invicta* in the US has been hindered by the tremendously widespread distribution of the target species. As with other invasive species, the chances of successful ant eradication decrease dramatically with increasing distribution (Myers et al. 2000; Rejmanek and Pitcairn 2002). In cases where ant ranges remain small, however, containment may be feasible and even eradication may be possible. In at least one such example, the Little Fire Ant, *Wasmannia auropunctata* (Roger), was eradicated from Santa Fe Island in the Galapagos (Abedrabbo 1994), and other eradication attempts are underway in New Zealand and Australia. Unfortunately, techniques for complete eradication can take years to develop. The results of this study suggest that in specific situations

where invasive ant colonies are still limited in distribution, non-target effects have been carefully considered and the prevention of additional colonization events has a high probability of success, temporary containment may be achieved by applying bait and toxicant treatments to expanding colony margins. At Haleakala National Park, we have implemented this technique on a larger scale while we continue to explore and test methods of eradication for the Argentine ant.

To our knowledge, efforts aimed at stopping colonies of invasive ants from spreading into natural areas are extremely rare. We believe, however, that containment as a general management technique is not only a potential stopgap for invasive ants, but can also have wider applications in conservation. For instance, large-scale eradication programs sometimes incorporate containment strategies and work from the edges of a species' distribution towards the middle, as in the case of the plant pest *Striga asiatica* in the US (Eplee 1992). Other situations involving invasive vertebrates can be imagined, wherein an incipient population temporarily restricted to a habitat patch might be fenced off from nearby suitable habitat before eradication is attempted. In all cases, the feasibility of outright eradication should be considered from the outset, but managers should also keep in mind that an intermediate containment program, tailored to the natural dispersal behavior of the target species, may increase their chances of future success even when methods for eradication are not immediately available.

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