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Indirect effects of ant eradication efforts on offshore islets in the Hawaiian Archipelago

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Abstract Invasive species eradication and control are considered vital components of the conservation, restoration, and management of many native ecosystems. Invasive ants, which are notoriously difficult to eradicate, can cause catastrophic changes in ecosystems and are aggressive colonists. Here we report the eradication and control of two widely distributed invasive ants and subsequent unanticipated effects on arthropod and avian communities. We used a paired experimental design that included 1 year of baseline data collection, to test the effects of the formicide hydramethylnon on abundances of two ant species on two pairs of offshore islets. *Pheidole megacephala* was eradicated from the treated islet in pair 1 and was not detected during 2003–2008. On pair 2 *Solenopsis*

geminata numbers declined, but the species remained present. Target ant densities remained high on untreated islets. Application of hydramethylnon reduced numbers of alien cockroaches (Order: Blattaria), but we did not detect effects on other nontarget arthropods. The eradication of *P. megacephala* was followed by dynamic compositional changes in the ant community, including the apparent colonization by three species (S. geminata, Tetramorium bicarinatum and Anoplolepis gracilipes) previously undetected on the islet. One of these, A. gracilipes, underwent a rapid range expansion during 2006–2008 which corresponded with reduced seabird nesting success. We conclude that hydramethylnon can be used effectively to eradicate P. megacephala. However, ant eradications can have detrimental effects on ecosystems and the potential for subsequent colonization of sites by other ant species that may be more harmful and more difficult to eradicate needs to be considered.

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Introduction

Eradication of invasive species is a vital part of the conservation and management of ecosystems (Myers et al. 2000; Ruiz and Carlton 2003). There have been



advances in the eradication of some groups (e.g., rats) from increasingly large islands (Howald et al. 2007), but for the majority of species, eradication remains more challenging (Clout and Veitch 2002), and for some species, such as invasive ants, it is notoriously difficult and requires ongoing treatment (Holway et al. 2002). This has global significance as hundreds of invasive ant species are undergoing human-mediated range expansions (McGlynn 1999; Holway et al. 2002). These invasions can alter the structure and functioning of natural communities (Christian 2001; Holway et al. 2002; Hill et al. 2003; O'Dowd et al. 2003; Krushelnycky and Gillespie 2008) and can be catastrophic to native biota by reducing, extirpating and possibly causing the extinction of arthropod species (Perkins 1913; Risch and Carroll 1982; Cole et al. 1992; Gillespie and Reimer 1993; LaPolla et al. 2000; Hill et al. 2003; O'Dowd et al. 2003), directly and indirectly harming vertebrates (Meek 2000; Holway et al. 2002; Davis et al. 2008; Plentovich et al. 2009) and altering plant communities (Bach 1991; Green et al. 1997; Christian 2001; Hill et al. 2003; O'Dowd et al. 2003; Handler et al. 2007). Endemic biota, especially those in areas such as the Hawaiian Islands where ants are believed to be absent from the native fauna, seem to experience the most significant losses (Perkins 1913; Zimmerman 1970; Howarth 1985; Cole et al. 1992; Gillespie and Reimer 1993; LaPolla et al. 2000; Krushelnycky and Gillespie 2010).

Historically ant eradication efforts met limited success, sometimes resulting in a temporary reduction in ant numbers followed by a sharp rebound (Williams et al. 2001; Tschinkel 2006). Recent successes include the eradication of Wasmannia. auropunctata (little fire ant) from 3 ha on Santa Fe Island (Abedrabbo 1994) and 21 ha on Marchena Island (Causton et al. 2005) both in the Galapagos archipelago, eradication of P. megacephala (big-headed ant) from treated pineapple plantations in Hawaii (Reimer and Beardsley 1990), and eradication of multiple infestations of Pheidole megacephala and Solenopsis geminata (tropical fire ant) from approximately 30 and 3 ha, respectively around human settlements in Kakadu National Park, Australia (Hoffmann and O'Connor 2004). These successes indicate that eradication is possible for certain species and circumstances given early detection of small, well-delineated infestations followed by rapid response and intensive management. However, in all of these cases there was at best only limited monitoring of the effects of reduced ant densities and the eradication process itself on non-target organisms with the exception of other ant species.

Attempts to eradicate or control ants often involve the broadcast of chemical ant baits or use of bait stations (Reimer and Beardsley 1990; Zerhusen and Rashid 1992; Green and O'Dowd 2010). Ants are known for their efficient exploitation of available food sources (Holldolbler and Wilson 1990) and can quickly transport bait underground before it is ingested by other arthropods. This preemption of bait is thought to minimize effects to non-target arthropods and therefore non-target effects may be more pronounced if baits are broadcast in areas with low densities of ants. However, this hypothesis has not been well studied and some evidence suggests that the broadcast of formicides can negatively affect non-target organisms (Green and O'Dowd 2010). Limited data on the impacts of hydramethylnon, a commonly used formicide, on non-target species indicate no changes in populations of non-target species in pine forests in the southeastern US (Colby 2002) and no effects when applied topically to Apis mellifera (European honeybee) (NPIC 2002). However, hand broadcast of hydramethylnon (tradename: MaxForce) on 6 ha Spit Island, Midway Atoll resulted in reduced numbers of alien cockroaches (Blattaria) and alien crickets (Orthoptera: Gryllidae, Plentovich et al. 2010).

The Hawaiian Islands, including islets offshore, provide opportunities to study the feasibility, effectiveness, and ecological cost of ant control methodology. Their isolation and small size increase chances of successful eradications and make recolonization more difficult. Because ants are believed to be absent from the native fauna (Wilson 1996), there is no risk for nontarget effects on native ant species. At least fifty species of invasive ants are established in Hawaii (http://www.antweb.org/hawaii.jsp). Pheidole megacephala and other species such as Anoplolepis gracilipes (yellow crazy ant) and S. geminata dominate lowland areas (Nishida 1992; Gillespie and Reimer 1993; Wilson 1996; Krushelnycky et al. 2005). Here we attempted to eradicate two of these species while carefully monitoring the non-target effects of the formicide application, as well as the non-target effects of reduced ant densities following treatment. Identification and quantification of non-target effects



will help managers determine ecological costs of control efforts and assess whether such efforts are warranted. Our specific objectives were to (1) eradicate two dominant lowland ant species, big-headed ant (*P. megacephala*) and tropical fire ant (*S. geminata*) from small (<5 ha) islets offshore of Oahu, Hawaii, (2) assess the effects of the formicide AMDRO® (active ingredient hydramethylnon) on non-target arthropods, and (3) quantify subsequent potential indirect effects of reduced target ant numbers on other ant species and on number of nesting seabirds.

Methods

Study sites

Based on the results of preliminary surveys we selected two pairs of offshore islets (Pair 1: Popoia/Mokuauia and Pair 2: Moku Iki/Moku Nui, Table 1, Fig. 1). Each pair was similar in location, topography, geology, vegetation composition, number of nesting seabirds, and ant species (S. Plentovich pers obs.). Members of pair 1 are flat, rocky and densely vegetated. Both islets sit between 265 and 350 m offshore of Oahu. They are dominated by the native plant Sesuvium portulacastrum. Scaevola taccada and the introduced species Portulaca oleracea and Asystasia gangetica are also common. Mokuauia is the larger of the pair with an area of 3.85 ha (11.7 acres). Popoia has an area of 1.56 ha (3.85 acres). The arthropod community on both islets in pair 1 was dominated by the big-headed ant (Pheidole megacephala).

Members of pair 2, known collectively as the Mokulua or twin islets are located approximately 1.05 km off Lanikai Point on the east side of Oahu (Fig. 1). The larger, Moku Nui is 4.84 ha with an elevation of 68.6 m, while Moku Iki is 3.35 ha with an elevation of 45.7 m. The combined effects of

steep, rocky terrain, soil disturbance by burrowing seabirds and approximately 5 years of drought (ending in 2004) left the Mokulua sparsely vegetated. The most abundant plant species on the islets were the alien grasses Cenchrus echinatus and Chloris barbata, along with the following native species; Jacquemontia ovalifolia subsp. sandwicensis, Sida fallax, Scaevola taccada, Sesuvium portulacastrum, and Chenopodium oahuense. The arthropod community on both islets was dominated by two species: the tropical fire ant (S. geminata) and the crazy ant (Paratrechina longicornis). Solenopsis geminata and P. megacephala were targeted in this study due to anecdotal observations of these two species attacking seabirds in the Hawaiian archipelago (A. Hebshi and C. Vanderlip pers obs.)

Ant control

We attempted to eradicate targeted ant species on one randomly chosen islet in each pair (i.e., Mokuauia and Moku Nui) using the formicide AMDRO[®] (active ingredient: hydramethylnon). AMDRO[®] is commonly used in the southeastern United States to control the red imported fire ant, *Solenopsis invicta* (Tschinkel 2006). It has been used in agroecosystems in Hawaii to eradicate *P. megacephala* (Reimer and Beardsley 1990). In February 2003 and 2004 we used a power blower and "Whirley Bird[®]" hand-held spreaders to broadcast AMDRO[®]. The broadcasts were carried out according to manufacturer's specifications with 1–2 lb (453–907 g) of formicide applied per acre (0.4 ha).

Monitoring

Long-term monitoring of ants

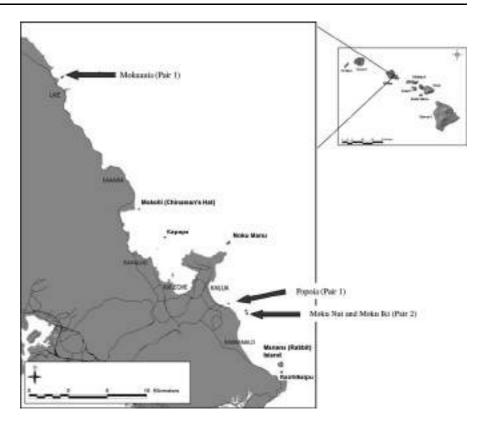
Ants densities were monitored using pitfall traps and bait cards. Fifteen pitfall traps were placed at

Table 1 Summary of treated and untreated islets in Pair 1 and 2 located offshore of eastern Oahu in the main Hawaiian Islands

Pair#	Treatment	Name	Target ant species	Size (ha)	Characteristics
1	Untreated	Popoia	Pheidole megacephala	1.56	Flat, heavily vegetated
1	Treated	Mokuauia	Pheidole megacephala	3.85	Flat, heavily vegetated
2	Untreated	Moku Iki	Solenopsis geminata	3.35	Steep, sparsely vegetated
2	Treated	Moku Nui	Solenopsis geminata	4.84	Steep, sparsely vegetated



Fig. 1 Location of four islets offshore of the windward coast of Oahu, Hawaii (lat: 21 N, long: 157 W) used as sites to study the effects hydramethylnon on bigheaded ant (*Pheidole megacephala*) and tropical fire ant (*Solenopsis geminata*) populations. Mokuauia and Moku Nui were the treated islets and Popoia and Moku Iki were the untreated islets



randomly selected, permanent sampling points. Pitfall traps (diameter: 6 cm, volume: 0.177 l) were set for 5 days at 3-month intervals during February 2002–January 2004, with a gap between January 2003 and May 2003. We also set bait cards to determine how treatments affected dominant ant species. Fifteen index cards (12.7 × 7.6 cm) were set along a transect bisecting each islet. Index cards baited with potted meat (i.e., SPAM®), peanut butter, and honey were set six times on each pair simultaneously between January 2003 and January 2005. Pair 1 was resampled in November 2006. The dynamic nature of the ant community on the treated islet in pair 1 led us to continue sampling until August 2008 (Fig. 3).

Seabird monitoring

We monitored the number of wedge-tailed shearwater chicks surviving until the approximate time of fledging once a year during 1996–2008 by counting chicks present in burrows in permanent plots. Counts from six to eight 50 m² plots on both islets of pair 1 and ten to twelve 20 m² plots in pair 2 were conducted in October and/or November of each year.

Short-term monitoring to determine the effects of AMDRO[®] on non-target arthropods

We assessed the effects of AMDRO® on non-target arthropods in April and May 2005 by treating 50% of each previously untreated islet in each pair (i.e., Popoia and Moku Iki, respectively) with AMDRO®. Twenty points (10 untreated and 10 treated) were randomly established on each islet. Points were separated from each other and the treatment boundary by at least 10 m. We sampled relative abundance and species composition of arthropods using pitfall traps at each point immediately before and 2 weeks and 4 weeks after treatment. Pitfall traps were left open for 2 days during each sampling period.

We expected ants and any non-target arthropods which ingested the bait to die within 2 weeks of application (Taber 2000), so we assumed any changes observed in arthropod numbers at the 2 and 4 week intervals were due to the application of AMDRO® rather than the indirect effects of reduced ant densities. We considered the possibility that highly mobile insects could move into treated plots and thus bias the findings towards no impact on these species.



However, the majority of highly mobile insects on these sites are flower-visiting species that utilize floral resources and would not ingest the soybean oilbased bait.

Statistical analysis

We compared numbers of targeted ant species present in pitfall traps over time on control and treatment islets using a mixed model analysis of variance (ANOVA) that included data from both islets. Data were analyzed with "islet" (i.e., treated/untreated), "before/after" treatment, "date" and sampling "point" as main effects and a "before/after" × "islet" interaction term. To control for variability among sampling points, "point" was nested in "Islet" ("point[Islet]"). To control for variability among dates, "date" was nested in "before/after" ("date[before/after]"). If the application of AMDRO® did have an effect on the abundance of *S. geminata* on the treated islet, we would expect to see a significant interaction between "islet" (i.e., treatment) and "before/after".

Changes in community composition of ant species were detected using a multi-response permutation procedure (MRPP) to test the null hypothesis that, based on relative Sorensen distance, there was no difference in ant community composition on treated and untreated islets (Mielke and Berry 2001; McCune and Grace 2002). MRPP is a nonparametric permutation method that is used to test the probability that there is no difference between groups. MRPP provides an estimate of effect size (A) and a test statistic (T). An A score of 1 represents perfect agreement in taxa identity and abundance between groups (i.e., islets). An A score of 0 indicates random between group agreement. Negative values indicate agreement between groups that is less than predicted by chance (McCune and Grace 2002). This analysis was done twice for each pair, a comparison of control and treatment islets before and again after treatment. Data from pitfall traps were relativized by total abundance for each trapping period. Relativization emphasizes differences in proportion between treated and untreated plots by reducing the influence of the most abundant species (McCune and Grace 2002). Rare species (<5% of samples) were deleted to enhance detection of compositional relationships (McCune and Grace 2002).

We tested the short-term effects of AMDRO® on numbers of non-target arthropods using a mixed model ANOVA with pooled data from treated and untreated plots on both islets. Data were analyzed with "islet", "before/after" (i.e., observations collected before or after treatment), sampling "point" and "treatment" as main effects with a "treatment" × "before/after" interaction term. To control for variation among sampling points, "point" was nested within "islet" (i.e., "point[islet]"). The response variable was the average of the two post-treatment samples at each point. If AMDRO® did have an effect on the abundance of non-target groups, we would expect to see a significant interaction between "treatment" and "before/after".

To test for changes in the number of nestling wedgetailed shearwaters on Popoia and Mokuauia before and after the appearance of A. gracilipes on Mokuauia, we used a mixed model ANOVA that included data from both islets. "Islet", "before/after" (i.e., before or after invasion by A. gracilipes) and sampling "point" were main effects and there was an "islet" × "before/after" interaction term, "Point" was nested within "islet" to control for variation in the number of seabird nestlings among points. If the presence of A. gracilipes had an effect on the number of seabird nestlings, we would expect a significant interaction between "islet" and "before/after". The number of seabird nestlings at each of the 14 points (eight points on Mokuauia and six points on Popoia) was averaged for the period before and after invasion by A. gracilipes giving us a total of 28 data points. Average number of nestlings was the response variable. The 2004 and 2005 data were removed from this analysis because of the intervening detection and eradication of a small population of rats (Rattus rattus) on Mokuauia (unpublished data). Average values are given as mean \pm standard error and we considered differences to be significant at an alpha of less than 0.05. ANOVAs and univariate tests were performed using JMP version 8 (SAS Institute Inc.). Community analyses were performed using PC-ORD version 5.21.

Results

Ant control-pair 1

In 2002, *P. megacephala* occurred in extremely high densities on both islets in pair 1 and was clearly the



dominant arthropod with as many at 6,864 individuals occurring in a single pitfall trap set for 5 days (Fig. 2). There was no difference in ant community composition prior to treatment (MRPP; Test statistic: T=0.308, A=-0.001, P=0.502). Following application of AMDRO® on Mokuauia in February 2003 P. megacephala was not observed on bait cards set during 2003–2008 or in pitfall traps set at 3-month intervals during 2003–2005 (Figs. 2, 3). During this same period densities remained high and P. megacephala remained the dominant ant species on Popoia, the untreated islet (Figs. 2, 3). Changes in community composition followed the removal of

P. megacephala from the treated islet as indicated by data from pitfall traps (MRPP; T = -63.88, A = 0.34, P < 0.001, Fig. 2) and bait cards (Fig. 3). A short period (~ 30 days) when no ants were detected was followed by substantial increases in *Ochetellus glaber* and *Plagiolepis alluaudi*, and the appearance of *S. geminata* during November 2003–January 2005 (Figs. 2, 3). By November 2006, the treated islet was dominated by two different species of ants (*A. gracilipes* and *Tetramorium bicarinatum*) concentrated in different parts of the islet (Fig. 3). Although *T. bicarinatum* was found in relatively large numbers in 2006, *A. gracilipes* became

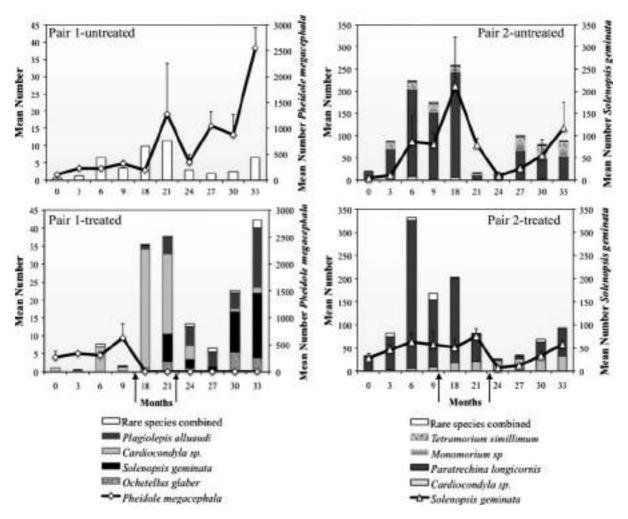


Fig. 2 Change in mean number of nontarget (first vertical axis) and target ants + mean standard error (second vertical axis) observed on two pairs of offshore islets before and after treatment (note *arrows*) of one member of each pair with the formicide hydramethylnon. Mean values were generated using

15 pitfall traps set on each islet every 3 months from February 2002 (month "0") to November 2004 (month "33") with the exception of February and May 2003. Rare species (i.e., mean/pitfall trap <1) were pooled to emphasize compositional changes. Note differences in scale



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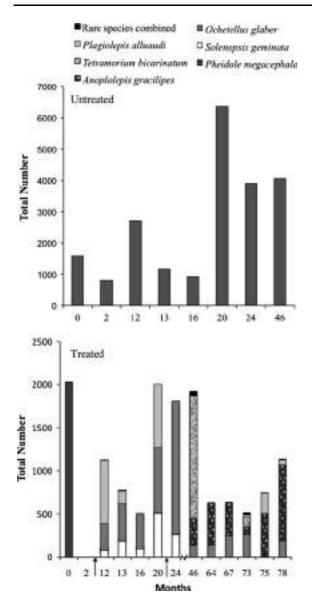


Fig. 3 Comparison of compositional changes in the ant communities of the untreated islet, Popoia (*top*) in Pair 1 over a 46-month period versus the treated islet, Mokuauia in Pair 1 (*bottom*) over a 78 month period. Changes were detected using cards baited with peanut butter, honey and SPAM[®]. Cards were placed before and after application of AMDRO[®] on the treated islet in February 2003 (month "1") and 2004 (month "13", note *arrows*). Note differences in the scale of the *y*-axis and categorical nature of the *x*-axis

progressively more numerous and widespread from November 2006 to August 2008 displacing *T. bicarinatum* (Fig. 3). Overall, ten species of ants other than *P. megacephala* were identified in low densities in pitfall traps and on bait cards on Mokuauia prior to the application of AMDRO[®].

Following the application, 15 species, including seven of the original species and eight species not previously found on the islet, were detected in pitfall traps and on bait cards.

The appearance and subsequent increase in A. gracilipes on the treated islet corresponded with significant declines in the number of seabird nestlings compared with the untreated islet, Popoia. This is implied by the significant interaction between "islet" and "before/after" (i.e., before and after invasion by A. gracilipes) in the mixed model ANOVA (F = 5.10, df = 1, P = 0.034). "Before/after", "islet", and "point[islet]" were not significant effects. The number of nestlings counted remained relatively constant on the control islet in Pair 1 (Popoia) throughout this period, and fluctuated similarly on the pair 2 islets that were not part of this analysis (Fig. 4).

Ant control-pair 2

Results were substantially different on the second pair of islets, Moku Iki and Moku Nui, where S. geminata was targeted. In 2002, S. geminata occurred in high densities in pitfall traps on both islets in pair 2 and was the dominant arthropod with as many at 3,911 individuals occurring in a single pitfall trap set for 5 days (Fig. 2). When data throughout the time series were analyzed, the significant interaction between "islet" and "before/after" indicated that the application of AMDRO® reduced abundance of S. geminata on the treated islet relative to the untreated islet (mixed model ANOVA; F = 4.66, df = 1, P = 0.032, Fig. 2). The "before/ after" effect was also significant indicating a change in S. geminata abundance in the period before and after application on both islets (mixed model ANOVA; F = 9.58, df = 1, P = 0.0023). "Islet", "date[before/After]", and "point[islet]" were not significant effects. Prior to application of AMDRO® relative abundance was similar between the two islets (Fig. 2). There was a marked increase in relative abundance of S. geminata following application on the untreated islet and, conversely, a small decrease on the treated islet (Fig. 2). Relative abundance on the treated islet tended to be lower for the remainder of the time series, but differences were not as pronounced (Fig. 2). The treatment effect was significant, but temporary and the species remained



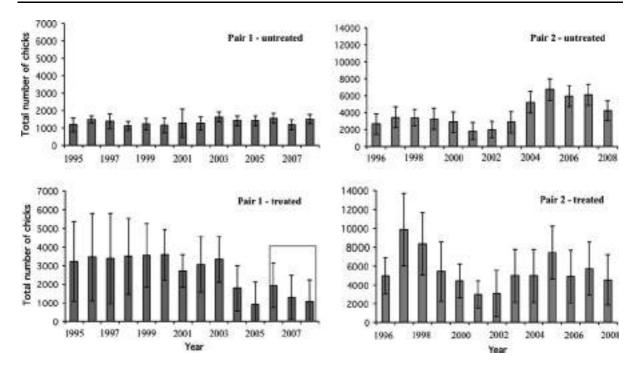
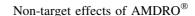


Fig. 4 Total number of breeding seabirds ± 95% confidence interval present on Pair 1 (Popoia and Mokuauia) and Pair 2 (Moku Iki and Moku Nui). Seabird breeding success declined significantly following the invasion of Mokuauia by

Anoplolepis gracilipes in 2006 (see box). Declines in 2004 and 2005 were attributed to a rat predation. Rats were eradicated before the start of the seabird breeding season in 2006

present on the islet even after an additional application in February 2004 (Fig. 2).

Despite this decline in S. geminata numbers, the overall species composition of the ant community remained relatively constant on each islet with the exception of the presence of Tetramorium simillimum and Monomorium floricola on the untreated islet. These species were consistently present on the untreated islet, but not the treated islet and were the reason for differences in ant community composition between islets before (Test statistic: T = -4.56, A = 0.021, P = 0.0046) and after (Test statistic: T = -7.89, A = 0.038, P = 0.0002) treatment. In 2002, prior to treatment, 15 ant species were collected in pitfall traps and on bait cards on the treated islet, Moku Nui, and 17 species were collected on untreated islet, Moku Iki. Following treatment, 15 and 16 species, respectively were collected on the treated and untreated islets. Overall, dominant species remained unchanged throughout the study (Fig. 2). The number of seabird nestlings fluctuated similarly on both control and treatment islets (Fig. 4).



We tested ten arthropod orders to determine if the application of AMDRO® had negative effects on non-target groups (Table 2). We also tested specific families including Diptera: Sciaridae and Hemiptera: Lygaeidae based on feeding behaviors that could potentially expose them to the formicide, (e.g., seed or fungus eaters). Only Blattaria showed a treatment effect. Blattaria numbers on the untreated points increased over time, while numbers on the treated points remained similar (Table 2). When data throughout the time series are analyzed, the significant interaction between "treatment" and "before/ after" indicated that the application of AMDRO® reduced abundance of Blattaria on the treated islet relative to the untreated islet (mixed model ANOVA: F = 4.01, df = 1, P = 0.049). The "Islet" effect was also significant indicating a difference in Blattaria abundance on each islet (mixed model ANOVA: F = 36.56, df = 1, P < 0.0001). This is not surprising due to the abundance of alien cockroaches on Moku Iki (Mean \pm SE = 43.0 \pm 9.17 before



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Table 2 Mean number \pm mean standard error of arthropods collected in pitfall traps before and after application of the formicide hydramethylnon on treated and untreated plots

Order	Mean (control)		Mean (treatment)	
	Before	After	Before	After
Blattaria	26.25 ± 7.68	48.13 ± 12.25	20.25 ± 8.1	22.5 ± 6.33*
Coleoptera	3.4 ± 0.71	5.5 ± 1.16	1.5 ± 0.41	3.3 ± 0.50
Collembola	26.6 ± 5.98	49.95 ± 25.29	22.3 ± 7.46	39.05 ± 11.08
Dermaptera	0.7 ± 0.40	0.9 ± 0.25	0.55 ± 0.22	0.78 ± 0.32
Diptera	4.3 ± 1.57	1.2 ± 0.34	2.2 ± 0.93	1.38 ± 0.36
Hemiptera	8.9 ± 2.24	2.9 ± 0.85	2.55 ± 0.94	5.4 ± 2.21
Isopoda	44.5 ± 12.3	60.82 ± 21.30	88.4 ± 27.27	95.28 ± 29.03
Orthoptera	8.45 ± 2.54	5.22 ± 1.84	9.25 ± 2.90	12.05 ± 4.24
Psocoptera	0.9 ± 0.45	0.4 ± 0.10	0.20 ± 0.12	0.45 ± 0.12
Thysanoptera	0.9 ± 0.33	0.35 ± 0.10	0.35 ± 0.13	0.48 ± 0.12

A total of forty pitfall traps were set in April and May 2005 on the two previously untreated islets from each pair (i.e., Popoia in Pair 1 and Moku Iki in Pair 2) before and at 2 and 4 weeks after application. The number of individuals collected at 2 and 4 weeks were averaged to generate mean and standard error. Significant (P < 0.05) effects relative to pre-treatment abundance indicated by *

treatment) compared to Popoia (Mean \pm SE = 3.50 \pm 1.03 before treatment). The "Before/after" and "Point[Islet]" effects were not significant.

Discussion

Ant control and eradication

The absence of *P. megacephala* on our treated islet in pair 1 after 6 years of intensive sampling indicates that broadcast of hydramethylnon (AMDRO®) eradicated P. megacephala from the islet. Three other successful eradications were observed using AM-DRO® against P. megacephala: on agricultural lands up to 10 ha in size in Hawaii (Reimer and Beardsley 1990) and Africa (Zerhusen and Rashid 1992) and on 30 ha around human settlements in Kakadu National Park, Australia (Hoffmann and O'Connor 2004). Conversely, use of AMDRO® was not an effective eradication tool for S. geminata. On our second pair of islets S. geminata numbers declined temporarily, but the species remained present on the treated islet, Moku Nui, even after two, islet-wide broadcasts of AMDRO® (Fig. 2). This was confirmed using bait cards which were set out multiple times immediately after application (Plentovich et al. 2009), but which tend to be inferior to other passive trapping methods such as pitfall traps since they tend to detect dominant species. Hoffmann and O'Connor (2004) also attempted but failed to eradicate *S. geminata* from an area of approximately 3 ha using 10+ applications of AMDRO®. They successfully eradicated this species only after switching to an alternative pesticide (i.e., Diazinon).

Both P. megacephala and S. geminata readily accept AMDRO® so the differential outcomes observed here and by Hoffmann and O'Connor (2004) indicate that differences in other factors such as number of queens and resource distribution and connectivity among nests may be responsible. In this study, site-specific differences also may have contributed to the outcome. The more rugged and exposed islets in pair 2 made bait application more difficult which could have led to less thorough coverage. Less vegetation on islets in pair 2 may have resulted in reduced potency of AMDRO® as the bait's active ingredient, hydramethylnon, rapidly degrades in direct sunlight exposure (Stanley 2004). Also, lower densities of S. geminata on pair 2 when compared to P. megacephala on pair 1 may have resulted in a lower percentage of individuals encountering, ingesting and distributing the bait among colonies.

Effects of AMDRO® on non-target arthropods

Alien cockroach (Order Blattaria) numbers increased at untreated points while remaining similar at treated



points suggesting that the application of hydramethylnon has a negative effect on cockroach numbers (Table 2). Broadcast of a different formulation of hydramethylnon (tradename: MaxForce) on Spit Island, Midway Atoll resulted in reductions in cockroaches and crickets (Orthoptera: Gryllidae, Plentovich et al. 2010). We did not detect changes in density for the remaining orders; however, low numbers for some groups may have limited our statistical power in these cases (Table 2). Since very few native arthropod species remain on these islets (Plentovich unp. data), it is important to point out that effects of hydramethylnon on endemic Hawaiian species is unknown. Preemption of baits by ants would also prevent us from detecting non-target effects.

Unanticipated effects of removal of *P. megacephala*

As observed in other eradication attempts, our treatments were followed by unanticipated secondary effects on other members of the community (Zaveleta et al. 2001; Bergstrom et al. 2009). The eradication of P. megacephala in pair 1 was followed by pronounced fluctuations in the islet ant fauna. We observed increases in non-target ant species such as O. glaber and P. alluaudi, the apparent invasion by three new species (i.e., S. geminata, Anoplolepis gracilipes and Tetramorium bicarinatum) and the subsequent apparent extinction of one of the new invaders (S. geminata) (Figs. 2, 4). By November 2006, A. gracilipes and T. bicarinatum partitioned the islet spatially, as each species dominated bait cards on different halves of the islet. Subsequent sampling between November 2006 and 2008 indicated that A. gracilipes had become the dominant ant. Its range expanded into territory formerly held by T. bicarinatum and was present on the majority of bait cards while T. bicarinatum was not collected on bait cards or was only collected on a single card depending on the sampling date (Fig. 4).

Fluctuations in ant numbers and species are likely related to dispersal methods (budding vs. mating flights), differential abilities of each species to monopolize available resources [e.g., carbohydrates from sap-sucking insects (Hemiptera: Stenorrhyncha) that were tended by *P. megacephala*], and possibly order of colonization. *Pheidole megacephala* disperses

primarily by budding (e.g., mated females walk rather than fly to nearby areas to found colonies) which may hinder reinvasion of isolated sites (Holway et al. 2002). Solenopsis geminata uses mating flights and budding to colonize new sites (Holldobler and Wilson 1990), possibly enabling quicker re-colonization of areas near source populations. This could explain why *S. geminata* was observed relatively soon (~9 months) after the removal of *P. megacephala*. Although *A. gracilipes* is also thought to primarily reproduce by budding (Haines and Haines 1978), recent findings (Abbott 2004, 2006) suggest that this species also disperses via mating flights. Even so, this species was not detected on the islet until 46 months after removal of *P. megacephala*.

Differential abilities of each species to monopolize available resources may be related to density and ability to displace other ant species (Kirschenbaum and Grace 2008). The majority of species present on our sites are considered "tramp ants", most of which are polygynous omnivores capable of forming supercolonies (Holway et al. 2002). These characteristics make them highly capable of invading new ecosystems and monopolizing resources. Some species seem to be able to exclude or suppress others (Kirschenbaum and Grace 2008) and some species (e.g., A. gracilipes) have proven especially harmful to native ecosystems (Hill et al. 2003; O'Dowd et al. 2003, Davis et al. 2008, 2010; Matsui et al. 2009). The subsequent dominance of A. gracilipes demonstrates its superior ability to monopolize resources, which may be facilitated by agonistic interactions among ant species. Lab tests demonstrated very high interspecific aggression in P. megacephala and A. gracilipes, the numerically dominant ant species at field sites in Hawaii (Kirschenbaum and Grace 2008). Our data are consistent with these findings. Although A. gracilipes is capable of displacing other species (Fluker and Beardsley 1970; Greenslade 1971; Haines et al. 1994), it has not displaced P. megacephala on the flat, densely-vegetated uplifted limestone islets in the Hawaiian archipelago.

Assembly history can be important in structuring communities (Fukami 2004) and this may play a role in why *A. gracilipes* is not more widespread in mesic lowland habitat in Hawaii. *Pheidole megacephala* was first recorded in the Hawaiian archipelago in 1879, while the first record of *A. gracilipes* was not until 1952 (Krushelnycky et al. 2005). The earlier



establishment of *P. megacephala* could have precluded the establishment of *A. gracilipes* in some areas. The removal of *P. megacephala* may have enabled the successful colonization by *A. gracilipes* on the treated islet while *P. megacephala* remained dominant on the untreated islet. If assembly history does play a role, the presence of *P. megacephala* may make some ecosystems more resistant to invasion by other invasive ant species.

The 2006 colonization of Mokuauia by A. gracilipes coincided with a significant decline in the number of seabird chicks. An initial decrease in chick number in 2005 and 2006 is attributed to a brief invasion by the black rat (Rattus rattus), which was eradicated in 2006 (unpublished data). On Mokolii islet, also off Oahu, Hawaii, the number of Wedge-tailed shearwater chicks increased dramatically from 1 to almost 200 in 2 years post-rat eradication (Smith et al. 2006). A similar increase in Cory's shearwaters (Calonectris diomedea) and Audubon's shearwaters (Puffinis iherminieri) was observed after rat eradication (Pascal et al. 2003, 2008; Igual et al. 2006). We observed only a modest increase in the number of shearwater chicks following rat eradication in 2006 followed by subsequent declines coincident with the growth and expansion of A. gracilipes populations. From 2006 to 2008 the number of chicks dropped significantly on the treated islet. There was no such decline on the control islet, Popoia and chick numbers on Moku Iki and Moku Nui fluctuated similarly (Fig. 4). Declines would have been even more pronounced if we had excluded sampling points on Mokuauia not yet invaded by A. gracilipes, but it would not have changed the conclusion.

Anoplolepis gracilipes is known to attack and kill birds and mammals (Haines et al. 1994; Matsui et al. 2009), reduce nesting success and alter abundances and foraging behavior in forest birds on Christmas Island, Indian Ocean (Davis et al. 2008, 2010). The species has also been observed in large numbers on nesting seabirds, causing irritation, sometimes apparently leading to abandonment of colonies (Freare 1999; Eijzenga and Smith unp. data). On our study site, we observed A. gracilipes on adults in large numbers in invaded areas. The ants, which subdue prey by spraying formic acid (Holldolbler and Wilson 1990), seemed to cause irritation, especially around the eyes, of adult seabirds prior to egg laying. This lead to constant attempts to rid feathers of ants, which may result in abandonment of nests. Ants were also observed on eggs and chicks. In ecosystems dependent upon marine derived resources delivered via seabirds, reductions in seabird numbers cause profound changes starting at the base of food chains (Croll et al. 2005; Fukami et al. 2006; Maron et al. 2006). Reductions in seabirds due to invasion by rats and arctic foxes in New Zealand and the Aleutian Islands, respectively led to widespread changes in ecosystems including alteration of soil nutrient content, phase shifts in plant communities and changes in faunal species composition (Croll et al. 2005; Fukami et al. 2006; Maron et al. 2006). Ant species can be important interactors in island ecosystems and their successful management requires carefully crafted, integrated plans and sustained monitoring during and following management actions. In this case, the presence of one species (i.e., P. megacephala) may protect colonial nesting seabirds from A. gracilipes. Therefore, if protection of seabirds is the primary objective, ant eradication efforts may be unfounded in many areas unless multiple ant species can be removed simultaneously.

In conclusion, hydramethylnon can be used with minimal toxic effects on non-target arthropods to eradicate dense colonies of P. megacephala from isolated islands and areas with low risk of invasion by other invasive ants. Eradication of S. geminata seems to be considerably more difficult. Like Hoffmann and O'Connor (2004), we were unable to eradicate S. geminata even after repeated applications of AMDRO® and would not recommend it be used alone for this purpose. Complex ecosystem interactions need to be considered when conducting ant eradications due to the potential for unintended direct and indirect effects such as those reported here. In this case the eradication of P. megacephala was not worth the ecological cost and it is possible that the presence of P. megacephala precludes other, potentially more harmful ant species from invading some areas.

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