

Invasive ants compete with and modify the trophic ecology of hermit crabs on tropical islands

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Abstract Invasive species can dramatically alter trophic interactions. Predation is the predominant trophic interaction generally considered to be responsible for ecological change after invasion. In contrast, how frequently competition from invasive species contributes to the decline of native species remains controversial. Here, we demonstrate how the trophic ecology of the remote atoll nation of Tokelau is changing due to competition between invasive ants (*Anoplolepis gracilipes*) and native terrestrial hermit crabs (*Coenobita* spp.) for carrion. A significant negative correlation was observed between *A. gracilipes* and hermit crab abundance. On islands with *A. gracilipes*, crabs were generally restricted to the periphery of invaded islands. Very few hermit crabs were found in central areas of these islands where *A. gracilipes* abundances were highest. Ant exclusion experiments demonstrated that changes in the abundance and distribution of hermit crabs on Tokelau are a result of competition. The ants did not kill the hermit crabs. Rather, when highly abundant, *A. gracilipes* attacked crabs by spraying acid and drove crabs away from carrion resources. Analysis of naturally occurring N and C isotopes

suggests that the ants are effectively lowering the trophic level of crabs. According to $\delta^{15}\text{N}$ values, hermit crabs have a relatively high trophic level on islands where *A. gracilipes* have not invaded. In contrast, where these ants have invaded we observed a significant decrease in $\delta^{15}\text{N}$ for all crab species. This result concurs with our experiment in suggesting long-term exclusion from carrion resources, driving co-occurring crabs towards a more herbivorous diet. Changes in hermit crab abundance or distribution may have major ramifications for the stability of plant communities. Because *A. gracilipes* have invaded many tropical islands where the predominant scavengers are hermit crabs, we consider that their competitive effects are likely to be more prominent in structuring communities than predation.

Keywords *Anoplolepis gracilipes* · Exclusion · Carrion · Invasive ants · Trophic ecology

Introduction

An increasing number of studies detail how invasive species interrupt interactions on islands, periodically culminating in community collapse or ‘invasional meltdowns’ (Simberloff and Von Holle 1999). Within animal communities these meltdowns often involve predators such as rats (Kurler et al. 2008), snakes (Wiles et al. 2003), fish (Townsend 2003) or mustelids, including stoats, weasels or mongoose (Watari et al. 2008). Exotic predators such as these have often been cited as responsible for extinctions, whereas competition between exotic and native species is thought to have a much reduced impact (Davis 2003; Sax and Gaines 2008). How frequently competition from invasive species contributes to the decline of native species remains controversial.

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While competition between ant taxa has been widely documented (Hölldobler and Wilson 1990), competition between ants and other organisms has received much less attention. Brown and Davidson (1977) conducted one of few studies examining competition between ants and other organisms. They demonstrated that desert ants compete for seeds with rodents. Through exclusion experiments, Brown and Davidson (1977) confirmed that this competition influences the abundance and distribution of both ants and rodents. Such studies demonstrate that ants have the potential to compete with and influence the population dynamics of many other taxa.

The yellow crazy ant, *Anoplolepis gracilipes* (Smith), is one of the six most widespread, abundant and damaging of invasive ants (Holway et al. 2002). It has invaded continents and islands throughout the tropics and sub-tropics (Wetterer 2005) and in many of these areas has substantially modified the ant fauna (Hill et al. 2003; Abbott et al. 2007; Bos et al. 2008). *A. gracilipes* is an omnivorous scavenging-predator consuming arachnids, crustaceans, isopods, insects, molluscs and myriapods, as well as birds, reptiles and mammals (Haines and Haines 1978a; Gillespie and Reimer 1993; Feare 1999). Crustaceans have been severely negatively affected by invasions of *A. gracilipes*. O'Dowd et al. (2003) documented the extirpation of the endemic red land crab *Gecarcoidea natalis* from expansive supercolonies of *A. gracilipes* on Christmas Island, and this ant has also been reported to attack and kill crabs elsewhere (Green et al. 1999; Feare 1999). However, reports of *A. gracilipes* killing crabs are from areas in which *A. gracilipes* have reached extreme densities, compared with much lower densities in most areas of *A. gracilipes* invasion, including many Pacific islands (e.g., Ward and Beggs 2007). Where *A. gracilipes* occurs in low densities, workers might not be able to kill crabs and may instead compete with crabs for resources.

Ants coexist with land crabs on most oceanic islands, which is likely mediated by a variety of mechanisms. Morrison (2002) studied interspecific competition between native ants and hermit crabs on Bahamian islands. He suggested that despite hermit crabs being dominated by ants, the crabs appeared to coexist with ants via their ability to more rapidly discover food. Morrison (2002) also noted temporal partitioning in ant and crab foraging, enabling hermit crabs to access food when few ants were present. However, invasive ants such as *A. gracilipes* are known to both quickly discover and dominate food resources (Sarty et al. 2006), as well as to forage throughout both day and night (Haines and Haines 1978b; Abbott 2005). Considering their spatial and temporal ubiquity on Tokelau, we tested the hypothesis that *A. gracilipes* competes with and influences hermit crab abundance and distribution. We demonstrate how competition for carrion by this invasive

ant is changing the trophic ecology of hermit crabs on tropical islands.

Materials and methods

Tokelau lies 483 km north of Samoa in the Pacific Ocean (approximately 9°45'S, 171°35'W). The country is comprised of three low-lying coral atolls (Atafu, Nukunonu and Fakaofu) and has a total land area of approximately 12 km². The islands are narrow and low-lying (~5 m above sea level). Tokelau lies in the southeast trade wind belt and has a humid tropical climate displaying little seasonal variation (mean annual temperature 28°C, mean annual rainfall 3,000 mm). The islands are comprised of coral rubble of varying size with poorly developed soil. Vegetation on these islands occupies two zones: the beach-crest and the islet interior. The islet interior is composed primarily of the coconut palm (*Cocos nucifera*) mixed with other common tropical canopy trees (*Cordia subcordata*, *Pisonia grandis*, *Guettarda speciosa*, *Pandanus* spp.). Small coconut palms and trees form the forest understory, while the bird's-nest fern (*Asplenium nidus*) forms the ground cover. Where vegetation cover is dense, the soil content of the islet interior is dark brown to black in color, with high organic content derived from decaying vegetation and bird guano (Parham 1971). Closer to the shore, on the beach-crest, the vegetation becomes denser, lower and more diverse (e.g., *Scaevola taccada*, *Morinda citrifolia*, *Pandanus* spp., *A. nidus*, *C. nucifera*) with little or no soil (Hinckly 1969; Parham 1971).

Our work was conducted on eight islands of Nukunonu atoll: six with *A. gracilipes* present (Lalo, Motuhaga, Nukunonu, Te Fala, Te Puka I Mua and Tokelau Islands) and two without this ant (Te Fakanava and Te Palaoa Islands). These study sites were chosen so as to include locations where *A. gracilipes* were present and absent on both sides of the atoll (Supplementary Figure 1), in an attempt to limit the influence of unmeasured environmental factors. Nevertheless, our choice of study sites was constrained by the distribution of *A. gracilipes*, and we cannot rule out the possibility that distribution of crabs or their isotope signatures were influenced by unmeasured extraneous factors.

Distribution of ants and crabs on Tokelau islands

To examine the relationship between *A. gracilipes* abundance and hermit crab densities on islands, we carried out an initial survey in November 2004 on two islands invaded by *A. gracilipes* (Nukunonu and Pukapuka Islands). Two transects were established at least 30 m apart on each island, from 1 m above the high tide mark on the lagoon side to 1 m above the high tide mark on the ocean side. Hermit crab densities, and the activity and relative

abundances of *A. gracilipes*, were assessed at 20-m intervals along each transect. Hermit crab densities were quantified by placing one 2 m × 2-m quadrat at each 20-m interval along the transect and recording all hermit crabs within each quadrat. To assess the activity of *A. gracilipes*, we haphazardly placed five 10 cm × 10-cm white laminated cards with approximately 2 g of tinned tuna in oil in the center, within 2 m of the hermit crab quadrat. The bait cards were left undisturbed for 1 h and then the number of *A. gracilipes* was counted on each card. Both the ant and crab abundance data were not normally distributed (Shapiro–Wilk test, $P \leq 0.001$). Consequently we used a Spearman's rank correlation coefficient, a non-parametric alternative to Pearson's correlation, to determine if a correlation occurred between the number of hermit crabs and *A. gracilipes* observed across the two invaded islets.

Ant exclusion experiments

To determine if ants excluded hermit crabs from food resources, we used an experiment with a three-factor factorial design. The treatments were 'invasion status' (invaded and uninvaded), 'site' (shore and interior of islands) and 'ant exclusion' (ants excluded or allowed access to carrion bait). Ant access and exclusion bait stations on each island consisted of plastic containers (90 mm × 160 mm × 160 mm; H × L × W) dug flush with the ground surface and filled ~10 mm from the top with coral rubble. A flat rock was placed on top of the coral rubble in the center to act as an 'island' for the carrion bait, upon which approximately 4 g of tuna was placed. Each exclusion container was then filled to the top with seawater, which served to exclude all ant species, but created no barrier to all sizes and species of hermit crabs.

For analysis, the dependent variable was the total number of hermit crabs observed feeding on the carrion at hourly intervals over a 24-h period. Data were not normally distributed (Shapiro–Wilk test, $P < 0.001$) and were heteroscedastic (Levene's test, $P < 0.001$). Transformation did not solve the heteroscedasticity problems, so we also used a three-factor univariate variation of permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001; McArdle and Anderson 2001). PERMANOVA is a univariate or multivariate analysis of variance using permutation procedures to obtain P -values. It is suitable for any multifactorial ANOVA design, allowing for all pairwise multiple comparisons by permutation. The dependent variable was the total number of crabs observed in each replicate over the 24-h observation period. PERMANOVA test results return P -values (i.e., no F -statistic or degrees of freedom), as the null distribution is generated by permutations. We analyzed untransformed, unstandardized data, using the Bray–Curtis measure of dissimilarity, with 4,999 permutations

per test. A variation of Anderson's (2001) PERMANOVA was constructed to allow for an unbalanced design (Manly 1997).

Isotope analysis

To examine the diet of hermit crabs on *A. gracilipes*-invaded and -uninvaded islands, we examined naturally occurring nitrogen and carbon isotope ratios. The ratio of $^{15}\text{N}/^{14}\text{N}$ [or $\delta^{15}\text{N}$ (‰)] is especially informative as it is indicative of trophic level status (De Niro and Epstein 1981). To create a continuum of stable isotope ratios, we collected specimens of flora and fauna from a range of ecological trophic levels. From the eight study sites we opportunistically collected the three resident terrestrial hermit crab species (*Coenobita brevimanus*, *C. perlatus* and *C. rugosus*) and *A. gracilipes*. In addition, we collected lepidopteran larvae (herbivore), cockroaches (scavenger), millipedes (scavenger), spiders (predator), two resident ant species (*Tetramorium guineense* and *Paratrechina longicornis*) and fruit from four plant species, coconut (*Cocos nucifera*), nonu (*Morinda citrifolia*) and *Pandanus* species as well as *Guettarda speciosa*. Fruit was chosen for analysis because we frequently observed both crabs and ants to consume fruit from several tree species, but ants were never observed consuming leaves. Between 2 and 27 samples were collected for each taxa. For the larger animal species we removed the gut tissue so as to not skew results towards recent feeding. Smaller animal species were analyzed whole, but were starved for 12 h before processing. Animals were killed by freezing for 24 h. For the hermit crabs, we sampled white muscle from the large chela. Carbonates were removed by immersing the chela tissue in 1 N hydrochloric acid. Samples were then dried at 60°C. Carbon and nitrogen stable isotope analysis was performed using a Dumas elemental analyzer (Europa Scientific ANCA-SL) interfaced to an isotope mass spectrometer (Europa Scientific 20/20 Stable Isotope Analyzer).

No evidence for heteroscedasticity (Levene's test, $P \geq 0.139$) was observed with the isotope data. However, the carbon data did not conform to a normal distribution (Shapiro–Wilk test $P < 0.001$). Consequently, to test whether isotope ratios of the hermit crabs were significantly different between invaded and uninvaded islets, we used a two-factor univariate PERMANOVA. The two fixed factors were hermit crab species, and the presence or absence of *A. gracilipes*. The dependent variable was the stable isotope ratio in question.

Can *Anoplolepis gracilipes* kill hermit crabs?

Anoplolepis gracilipes could be influencing crab abundance by predation and/or competition. We used both field and

laboratory experiments to determine if extremely high numbers of *A. gracilipes* could kill hermit crabs. In field experiments, we placed hermit crabs in cages. Twelve hermit crabs of each of the three resident species (*Coenobita brevipennis*, *C. perlatus* and *C. rugosus*) were collected from the field and placed singly in a wire cage (150 mm × 150 mm × 120 mm; H × L × W; 10 mm × 10 mm gap size). The cages and crabs were then placed in areas the islands that had the highest density of *A. gracilipes*, as determined in the surveys and ant exclusion experiment. Crabs were left in these field cages for 48 h. In laboratory experiments, we placed individual *C. perlatus* into ten containers (90 mm × 160 mm × 160 mm; H × L × W) with entire *A. gracilipes* nests (~10,000 workers). The containers had Tanglefoot® applied to the top 15 mm to prevent ants from escaping. Crabs were left in these laboratory experiments for 72 h, and conditions assessed thereafter.

Results

Distribution of ants and crabs on Tokelau islands

The density of hermit crabs was negatively correlated with that of *A. gracilipes* across the island transects (Spearman's rank correlation $S = 4547.8$, $P = 0.003$, $r = -0.555$; Fig. 1a). We further examined the influence of *A. gracilipes* on hermit crabs of ants and densities of crabs at the periphery of the islands (1–20 m above the high-tide line) and the interior, at two central plots. Densities of crabs were lower in the center of the islands than on the shore areas, but this effect was pronounced on islands with *A. gracilipes* (Fig. 1b). Only one individual hermit crab was observed in our plots on the central areas of the *A. gracilipes*-infested islands. The activity and relative abundance of *A. gracilipes* were higher in these central areas than at the periphery of the islands (Fig. 1c).

Ant exclusion experiments

When present in sufficient numbers, *A. gracilipes* dominated food baits and repelled hermit crabs by spraying formic acid at them. Significantly fewer hermit crabs were able to access food baits on islands invaded by *A. gracilipes* than on those islands without *A. gracilipes* (PERMANOVA, $P = 0.002$; Table 1; Fig. 2). *A. gracilipes* competitively excluded crabs from carrion resources, as did other invasive ants to a lesser extent (on *A. gracilipes*-free islands). More crabs were able to access and remain at food baits when ants were excluded (PERMANOVA, $P < 0.001$). The effect of site (shore or interior plots) was marginally significant (PERMANOVA, $P < 0.051$). More

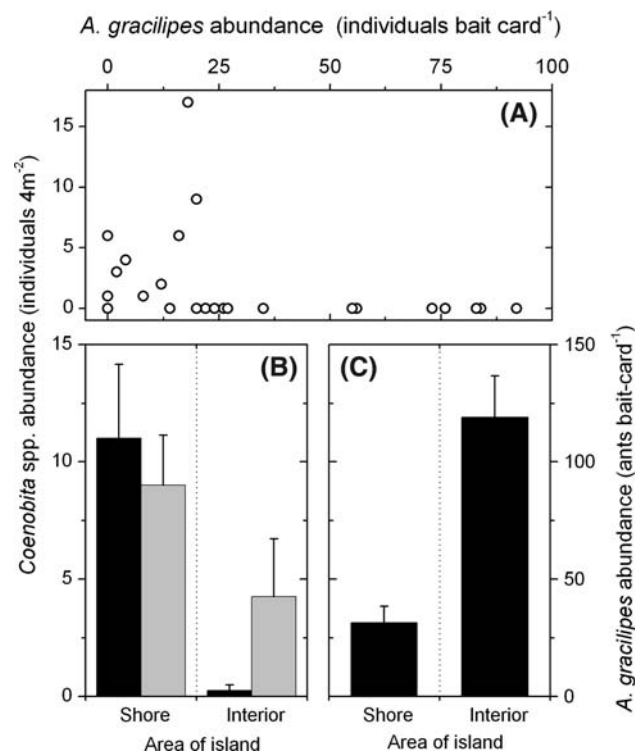


Fig. 1 The relationship between *A. gracilipes* and hermit crab abundances. **a** A scatter plot showing the correlation between the presence of hermit crabs in 2×2 m plots and the abundance of *A. gracilipes* on bait cards. **b** Bait card data from **a**, but showing the density of crabs on either side of the shore or periphery of the islands (1–20 m above the high-tide line) compared to two central plots. Data for islands with *A. gracilipes* (solid shading) and without these ants (grey shading) are shown. **c** Using the same subset of data, *A. gracilipes* are ~4× more abundant in central areas of the islands

Table 1 Full output from the PERMANOVA examining foraging by hermit crabs in ant exclusion experiments

Factor	<i>P</i> -value
Invasion status (<i>A. gracilipes</i> present or absent)	0.0024
Site (shore or forest interior plots)	0.0510
Ant exclusion (ants excluded or allowed on baits)	0.0004
Invasion status × site	0.3018
Invasion status × ant exclusion	0.4978
Site × ant exclusion	0.0020
Invasion status × site × ant exclusion	0.9684

PERMANOVA analysis gives results as *P*-values only

crabs were able to access food baits on shore plots than plots in the interior of the islands. This result corroborated with the higher numbers of *A. gracilipes* observed in the interior relative to shore areas during the survey. The other significant term in the PERMANOVA was a significant site × ant exclusion interaction (PERMANOVA, $P < 0.001$), indicating that the effects of ant exclusion on hermit crab foraging changed between shore and interior plots. This

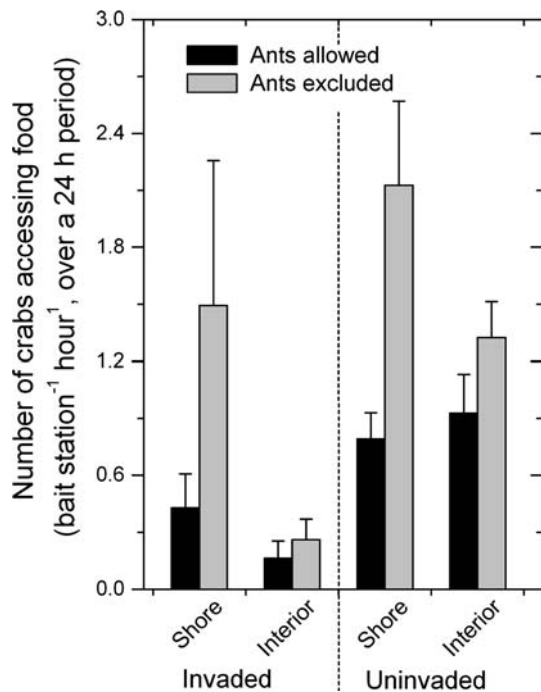


Fig. 2 The influence of ant exclusion on carrion use by hermit crabs. ‘Invaded’ and ‘Uninvaded’ refer to the presence or absence of *A. gracilipes*. ‘Shore’ and ‘Interior’ refer to forest patches near the beach or center of the island, respectively. All error bars are 1 SE

significant interaction was due to crabs displaying a low utilization of carrion in interior plots of islands invaded by *A. gracilipes*, irrespective of the exclusion treatment, relative to all the other areas.

Isotope analysis

According to $\delta^{15}\text{N}$ values, the three hermit crab species on Tokelau have a relatively high trophic level on islands where *A. gracilipes* had not invaded (Fig. 3). In contrast, on invaded islands we observed a significant decrease in $\delta^{15}\text{N}$ for all crab species (PERMANOVA, $P < 0.005$). We observed no significant differences in $\delta^{15}\text{N}$ between crab species, nor a significant crab species \times invasion status interaction ($P \geq 0.234$). Hermit crabs were feeding at a relatively lower trophic level in the presence of *A. gracilipes*. These results confirm our field observations, where only in the absence of *A. gracilipes* did we ever see hermit crabs feeding on dead birds, fish, lizards or other crabs.

Of the ant species examined, *P. longicornis* had the highest mean $\delta^{15}\text{N}$ value overall, while *T. guineense* and *A. gracilipes* had intermediate $\delta^{15}\text{N}$ signatures consistent with omnivory (Fig. 3). Cockroaches, caterpillars and millipedes had low $\delta^{15}\text{N}$ values. The fruits of *C. nucifera*, pandanus and *G. speciosa* all had nitrogen stable isotope signatures indicative of primary producers. However, the *M. citrifolia* (nonu) fruit had an unusually high mean $\delta^{15}\text{N}$ value, which

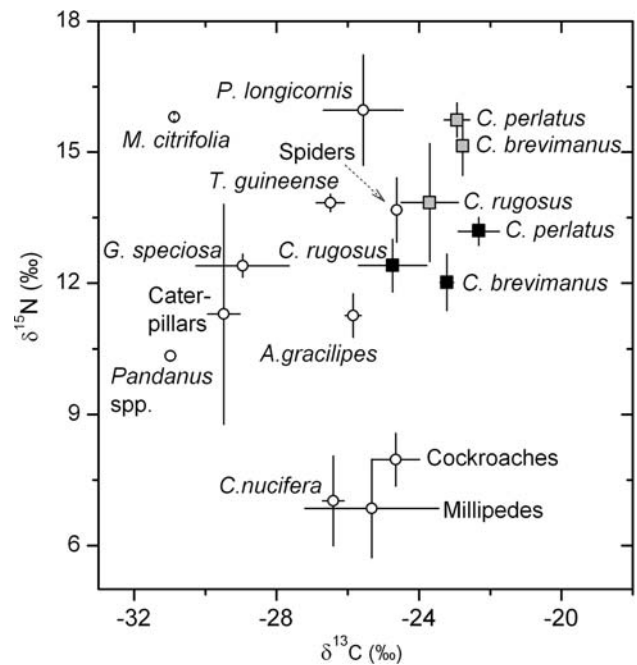


Fig. 3 $\delta^{15}\text{N}$ values for three hermit crab species significantly decrease in the presence of *A. gracilipes* (solid black squares) compared values from crabs on islands where *A. gracilipes* are absent (black squares with grey fill). The three terrestrial hermit crab species were *Coenobita brevimanus*, *C. perlatius* and *C. rugosus*. Open circles represent $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for other sampled taxa and include the ant species *A. gracilipes*, *Tetramorium guineense* and *Paratrechina longicornis*, lepidopteran larvae (herbivores), cockroaches, millipedes and spiders, and the plant species *Cocos nucifera* (coconut), *Morinda citrifolia*, *Pandanus* spp. and *Guettarda speciosa*. All error bars are 1 SE

did not reflect its expected trophic position as a plant. We are unsure of why this occurred and suggest that one possibility is that *M. citrifolia* has deep roots that allow these plants to have access to marine-derived nitrogen. Marine-derived nitrogen is enriched in $\delta^{15}\text{N}$ relative to terrestrial or freshwater nitrogen (Kline et al. 1990). However, because no hermit crab species were observed eating nonu, we feel that we can discount *M. citrifolia* as a potential influence on hermit crab $\delta^{15}\text{N}$ ratios.

There was no significant effect of the presence or absence of *A. gracilipes* on islands for the $\delta^{13}\text{C}$ values of hermit crabs (PERMANOVA, $P = 0.324$; Fig. 3). However, we did observe a significant difference in $\delta^{13}\text{C}$ values between hermit crab species (PERMANOVA, $P < 0.001$). Pairwise comparisons revealed a significant difference in $\delta^{13}\text{C}$ between *C. perlatius* and *C. rugosus* (PERMANOVA, $P = 0.005$), and *C. brevimanus* and *C. rugosus* (PERMANOVA, $P = 0.004$), but no significant difference between *C. perlatius* and *C. brevimanus* (PERMANOVA, $P = 0.374$). These results indicate that *C. rugosus* was obtaining its carbon from a different source than *C. perlatius* and *C. brevimanus*. Furthermore, there was no significant interaction between the presence or absence of *A. gracilipes* and

hermit crab species (PERMANOVA, $P = 0.123$). Therefore, all species of hermit crab appeared to be responding similarly to the presence of *A. gracilipes* in regards to carbon stable isotope signatures.

All of the fruits had similarly low carbon stable isotope signatures. Insects had a range of $\delta^{13}\text{C}$ values. Caterpillars had the lowest $\delta^{13}\text{C}$ signature of all the insects, while cockroaches had the highest values.

Can *Anoplolepis gracilipes* kill hermit crabs?

No hermit crabs were killed by *A. gracilipes* in laboratory or field experiments.

Of the 36 hermit crabs initially used in the field experiment, 14 escaped from their cages. Predation was not responsible for these disappearances as no shells of the hermit crabs were left in the cages (as would be expected if the disappearances were caused by ant predation).

Observations during the laboratory experiment showed individual *A. gracilipes* would immediately swarm over those hermit crabs placed inside nest containers, spraying formic acid into the crabs eyes and mouthparts. Hermit crabs would immediately retreat into their shells. The ants continued to look for the crab once it had withdrawn into its shell, and when unsuccessful, would leave. Workers would then not return to the crab until it moved, and then this process would start over again. When these ants came within a short distance of hermit crabs (several centimeters), hermit crabs would often swiftly withdraw into their shells.

Discussion

We observed competition between crabs and ants on naturally occurring carrion in our experiments. Both *A. gracilipes* and hermit crabs would arrive at and attempt to consume food items often within minutes of the food bait being offered. Ants would crawl over the crabs and spray acid on their heads. In areas of low *A. gracilipes* densities, this aggression was tolerated by the crabs to a degree enabling crabs to forage. When *A. gracilipes* were in high densities, their continual swarming and aggressive behavior would cause the crabs to quickly withdraw into their shells and move away from the food resource. The near complete absence of crabs from high density areas of *A. gracilipes* was not a result of predation by ants. The influence of *A. gracilipes* was density-dependent and resulted in the exclusion of crabs from interior areas of these tropical islands, but not at the periphery. The isotope analysis confirmed that the diet of hermit crabs was modified by these invasive ants, suggesting long-term exclusion from carrion resources.

Predation is widely considered as the primary mechanism for invasive species to modify recipient communities.

While predation is thought to account for 98% of all known extinctions associated with exotic species, competitive interactions between native and exotic species have rarely resulted in extinctions (Sax and Gaines 2008). Davis (2003) argues that the influence of competition by exotic taxa on native species is often much weaker than predation. These weaker interactions may allow time for resident taxa to modify their life-history patterns and coexist with exotic species. Examples of such niche adjustments include resident fish altering their foraging depths in response to invasive species (Ross 1991; Mooney and Cleland 2001). Our results suggest a similar niche adjustment by hermit crabs. The hermit crabs avoid areas with high densities of *A. gracilipes* and in the presence of these ants forage at a lower trophic level.

Morrison (2002) suggested that hermit crabs coexist with ants on Bahamian islands via two mechanisms. First, crabs discovered food faster than ants. Hermit crabs are renowned for their effective olfactory ability (Thacker 1996) and were clearly able to discover food quickly on Tokelau. However, *A. gracilipes* are similarly efficient in discovering food when workers were highly abundant (Lester and Tavite 2004; Sarty et al. 2007). Second, Morrison (2002) observed that reductions in ant foraging during the night enabled hermit crabs to access food when few ants were present. Our experiments would have identified any temporal variation in *A. gracilipes* abundance that might have enabled hermit crabs to obtain resources, but these ants foraged and controlled resources for the entire 24-h period of observation. High densities enable *A. gracilipes* to quickly find and dominate the vast majority of resources. When present in high numbers, these ants appear to be extremely competitive, and their influence on hermit crab communities becomes more apparent. We have similarly observed the assembly of Tokelauan ant communities to be dependent on the abundance of *A. gracilipes* (Lester et al. 2009).

There are two likely reasons why *A. gracilipes* is more abundant in the interior plots than shore plots. First, it is likely that there is more food there, and second, the lack of appropriate nest sites on the shore may limit the distribution of *A. gracilipes* on the shore. Previous research has shown that sugary, carbohydrate-rich liquids (in the form of plant and hemipteran exudates) form a high proportion of food brought back to the nest of *A. gracilipes* (Haines and Haines 1978b). Additionally, food choice experiments have shown *A. gracilipes* strongly recruits to sugary baits (Rao and Veeresh 1991; Sarty et al. 2007). Carbohydrates are crucial to the survival of *A. gracilipes* (Hölldobler and Wilson 1990), and insect exudates may be seen as the fuel for their high-tempo activities (Davidson 1998) and aggression (Grover et al. 2007). However, plant and insect exudates are low in abundance or absent on the shore compared to

the interior of islands (Parham 1971; personal observations). Thus, the absence of exudates may limit the abundance of *A. gracilipes* on the shore. For nest sites, *A. gracilipes* will generally use the base of trees, piles of dead vegetation (especially coconut husks), large rocks or relatively permanent structures (Haines and Haines 1978b). The shore is generally devoid of such places, primarily consisting of small coral rubble and regularly being inundated by waves during storms. In contrast, the interior of islets provides a multitude of nest sites and may also be a key factor in the high abundance of *A. gracilipes* in the interior.

What are the likely long-term effects of this change in the trophic ecology hermit crab populations of Tokelau? There are several islands in this atoll on which *A. gracilipes* are absent or in extremely low densities (Abbott et al. 2007). In the interior of islands where *A. gracilipes* are in high abundance, the isotope data indicate that crabs may have a reduced protein diet from carrion sources. Feeding at lower trophic levels may lower the relative fitness of crabs (Kennish 1996). However, the crabs may still access carrion and protein sources at the periphery of islands, as observed in our exclusion study. Thus, the population level effects of competitive for carrion on hermit crab populations are likely to be limited to a change in distribution on islands where *A. gracilipes* is present.

There are, however, likely to be several consequences of hermit crabs being excluded from the interior of invaded islets. Terrestrial hermit crabs have been shown to have significant impacts on plant establishment, distribution and abundance through their intense consumption of seeds and seedlings and their preferential predation of some species (Louda and Zedler 1985). Lindquist and Carroll (2004) concluded that differences in tree density and diversity in a coastal forest in Costa Rica were caused by variation in the abundance and distribution of land and hermit crabs. Similarly, Louda and Zedler (1985) suggest the intensity and patterns of seed predation by terrestrial hermit crabs may determine plant distributions and abundances on Enewetak Atoll in the Marshall Islands. The plants *G. speciosa* and *S. taccada* suffered severe damage by crabs (Louda and Zedler 1985). Both of these trees are common on Tokelau. Thus, the partial exclusion of terrestrial hermit crabs from the island interiors by *A. gracilipes* could indirectly release seedling recruitment, enhance species richness of seedlings and increase plant abundances. Similar results have occurred on Christmas Island when *A. gracilipes* extirpated the native 'keystone' land crab (O'Dowd et al. 2003).

There is clearly a deterministic aspect to the assembly of hermit crab and ant communities of Tokelau generated by competition with *A. gracilipes*. Competition by ants can influence the abundance of other animals many thousands of times their size (Brown and Davidson 1977), and subtle changes in a species abundance or function can have major

ramifications for communities (Louda and Zedler 1985; Lindquist and Carroll 2004). While the effects of biological invasions are often more apparent through predation (e.g., O'Dowd et al. 2003; Kurle et al. 2008), competitive effects can be more subtle. Because *A. gracilipes* has invaded many tropical islands where the predominant scavengers are hermit crabs, we conclude that their competitive effects are likely to be more prominent in influencing communities than predation. Similarly, many invasive ants are scavengers (Holway et al. 2002). We would be surprised if species such as the red imported fire ant (*Solenopsis invicta*) did not similarly compete with and structure scavenger communities, whether those scavengers are crabs, birds or other organisms.

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