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The Effect of Alien Predatory Ants (Hymenoptera: Formicidae) on Hawaiian Endemic Spiders (Araneae: Tetragnathidae)[1]

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ABSTRACT: The fauna of the Hawaiian Islands is characterized by spectacular species radiations with high levels of endemism, which is coupled with an extreme vulnerability to invasion by alien species. Of all alien invertebrate predators, ants are most notorious in their effect on native Hawaiian biota. This study examined distribution of ants in mesic and wet forests throughout the Hawaiian Islands and the extent to which they overlap the range of representatives of a lineage of endemic Hawaiian invertebrates, the genus *Tetragnatha* (Araneae: Tetragnathidae). Two species, *Pheidole megacephala* (F.) and *Anoplolepis longipes* (Jerdon), were implicated in the exclusion of native spiders from native and disturbed forest. One species, *Solenopsis papuana* Emery, showed extensive overlap in its range with that of the native spiders. However, we found a significant inverse relationship between the abundance of *S. papuana* in an area and the diversity of the indigenous *Tetragnatha*. Interactions between the spiders and the two species of ants, *P. megacephala* and *A. longipes*, were conducted in the laboratory and indicated that the spiders were very vulnerable to attack by these ants. Alien spiders appear to tolerate the presence of ants because they have either a strong exoskeleton, can appendotomize their legs, or else are capable of wrapping the ant in silk. Spiders that normally coexist with ants appear to use one or more of these methods for defense. The riparian existence of the genus *Tetragnatha* outside Hawaii may protect it from predation by ants. In Hawaii, where their habitat preference is no longer restricted to riparian sites, they may be extremely vulnerable to these alien predators.

THE EXTREME ISOLATION of the Hawaiian archipelago has allowed repeated and explosive diversification of species from a single ancestor, often accompanied by radical shifts in morphology, ecology, and behavior. Some of the best examples of this process can be found within the honeycreepers (Berger 1981, Freed et al. 1987), the land snails (Cooke et al. 1960), the crickets (Otte 1989), and the family Drosophilidae, a spectacular radiation with over 500 endemic species (Kaneshiro and Boake 1987). These radiations are associated with high frequencies of endemism: greater than 81% in birds (Shallenberger 1984) and an extraordinary 99% in terrestrial molluscs (Gagné 1988) and arthropods (Gagné and Christensen 1985).

Coupled with this extraordinary diversification within lineages is an increased vulnerability to perturbation and invasion from alien species, which is largely a consequence of their isolation from competition and predation from continental faunas during their evolutionary history. In addition, the heavily dissected terrain and enormous spatial variability in climate, which may have accelerated speciation considerably, has also resulted in species with very localized distributions (Simon et al. 1984). Many Hawaiian honeycreepers and land snails have gone, or are going, extinct, particularly at lower elevations

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(below 600 m). Unfortunately, we have virtually no information on the conservation status of the enormous array of endemic arthropods, which are being increasingly threatened by Hawaii's "Noah's ark of undesirable biota" (Gagné 1988). Included among the alien biota are 2000 arthropods, 50 land birds, 18 mammals, and ca. 900 plant species (Stone and Scott 1985, Moulton and Pimm 1986, Wagner et al. 1990). Some of these alien species feed on the native plants or interfere with their reproduction; others prey on, parasitize, or compete with native animals (Howarth 1985, Smith 1985, Stone 1985). Of all the alien invertebrate predators, ants are the most notorious in their effect on the native Hawaiian biota (Howarth 1985, Howarth and Medeiros 1989). Of the 35–41 species of ants currently established in Hawaii, the major threats to native fauna are generally considered to be the bigheaded ant, *Pheidole megacephala* (F.); the longlegged ant, *Anoplolepis longipes* (Jerdon); the Argentine ant, *Iridomyrmex humilis* (Mayr); and the fire ants *Solenopsis geminata* (F.) and possibly also *S. papuana* Emery (Reimer et al. 1990, Reimer in press). The possible importance of ants in the extirpation of native arthropods was recognized even at the beginning of this century (Perkins 1913). Since then, additional extinctions of native invertebrates have been attributed to ants, particularly at lower elevations on all the main Hawaiian islands (Zimmerman 1948, Solem 1976, Gagné 1979, Hardy 1981). However, all evidence to date is circumstantial: the only controlled studies on the interaction of the ants with native species have been preliminary assessments (Medeiros et al. 1986).

The study reported here examined the interaction between ants and endemic Hawaiian spiders of the genus *Tetragnatha*. In the Hawaiian Islands *Tetragnatha* is represented by a lineage of more than 60 taxa (R. G. G., unpublished data). Before 1991, only nine species had been described (Karsch 1880, Simon 1900, Okuma 1988). Gillespie (1991, 1992) has recently completed descriptions of an additional 16 species. In the study reported here we examined (1) presence of native tetragnathid spiders within the range occupied by ants of different species in wet and mesic habitats throughout the Hawaiian Islands; (2) relative abundance of ants and spiders at specific sites; (3) interactions between the spiders and two species of ants (*Pheidole megacephala* and *Anoplolepis longipes*) through behavioral observations in the laboratory using both native and alien spiders; and (4) attributes of Hawaiian *Tetragnatha* that could be used in defense against aggressive ants: (a) strength of exoskeleton: the exoskeleton may be impenetrable to ants; (b) leg appendotomy: the loss of a leg at a predetermined locus of weakness (Bonnet 1930, Roth and Roth 1984); (c) wrapping in silk: a common strategy used by spiders when confronted with large or dangerous prey is to wrap them in silk (Riechert and Luczak 1982).

MATERIALS AND METHODS

Presence of Native Spiders within Habitat Range of Ants in the Hawaiian Islands

To assess the extent of overlap between native spiders and different species of alien ants, and the possible exclusion of the spiders by the ants, we mapped the distribution of each species of ant found in wet and mesic forested areas throughout the Islands. We then compared the ant distributions with the distribution of native *Tetragnatha*. We used 10–20 sites at each of five elevational categories (0–300 m, 300–600 m, 600–900 m, 900–1200 m, 1200–1500 m) in native (dominated by naturally occurring plants), disturbed (heavily invaded by introduced plants), and alien (entirely introduced plants) habitats. The presence of ants was determined by visual observations and collection for specific identification. For a given site, observations of ants and spiders were made at the same (or similar) times of the year. We used a total of 18 sites on Kauai (Hanakapiai, 30 m; Hono O Na Pali, 150 m; Kanaele, 650 m; Kawaikoi, 1050–1120 m; Kokee, 1120 m; Kuia, 1000–1150 m; Puu Hinahina, 1040 m; Puu O Kila, 1040 m; Waiahuakua, 240 m; Waimea Canyon, 450–1040 m); 17 sites on

Oahu (Aiea Ridge Trail, 550 m; Kaena Point, 15 m; Konahuanui, 950 m; Manoa Falls, 275 m; Mt. Kaala summit, 1150–1220 m; Pahole Gulch, 580–700 m; Palikea, 910 m; Poamoho Trail, 610 m; Tantalus, 610 m; Waikane Trail, 360–610 m; Waianae Kai, 610 m); 1 site on Lanai (Munro Trail, 1000 m); 4 sites on Maui (Hanawi, 460 m; Kahului, 15 m; Kihei, 3 m; Kipahulu, 610 m); and 28 sites on Hawaii (Hualalai, 760–1370 m; Hawaii Volcanoes National Park, 915–1900 m; Kahaualea, 700–1100 m; Kealakekua, 915 m; Kipahoehoe, 420 m; Laupahoehoe, 425–915 m; Manuka, 400–1370 m; Pohakuloa, 2070 m; Punaluu, 0 m; Puu Makaala, 1100 m; Puu O Umi, 1220 m; Stainback Highway, 300–915 m). The same habitats were checked for the presence of native *Tetragnatha* at similar times of the year. The spiders were monitored by direct observation, while walking through an area after nightfall using headlamps (most endemic *Tetragnatha* are strictly nocturnal). Individuals were captured in plastic vials and taken back to the laboratory for identification.

Relative Abundance of Ants and Spiders at Specific Sites

Our aim in this part of the study was to determine the extent to which ants were found at the same site and time as native spiders, and the possible effects that ants might have on the species diversity, richness, and abundance of the spiders. At each of the sites listed below we monitored the abundance of both *Tetragnatha* spiders and ants during the same 24-hr period. The spiders were monitored by direct observation as described above, with abundance at a site being quantified by counting and collecting every spider observed (both adults and immatures) over a 1-hr interval. Ant abundance was monitored using unbaited pitfall traps as well as direct observations. Traps consisted of a plastic cup, 7.5 cm in diam., placed low in the ground so that the lip was flush with the surface of the soil. A small amount of ethylene glycol (which is virtually odorless and evaporates only very slowly) was placed in the bottom of each cup. A total of four traps were left at each site for the 24-hr period.

We monitored one to five sites at different elevations in native or disturbed forest on the following Islands: Kauai: Waimea Canyon at 610 m (dry), 1040 m (mesic), and 1220 m (wet); Waiahuakua at 400 m (mesic–wet); Wahiawa Bog at 650 m (wet); Kuia at 1010 m (mesic); Mohihi Ditch at 1070 m (mesic–wet); Koaie Stream at 1130 m (wet); and on the Department of Fish and Wildlife transect 5 at 1220 m (wet). Oahu: Waianae Kai at 580 m (mesic). Molokai: Kamakou at 1150 m (wet). Maui: Kipahulu at 610 m, 915 m, 1220 m, and 1525 m (all wet forest sites); Hanawi at 460 m (wet); Waikamoi at 1340 m (wet) and at 1590 m (wet); and Honomanu at 1980 m (wet). Hawaii: Laupahoehoe on the east slope of Mauna Kea at 340 m, 700 m, 990 m, 1280 m, and 1570 m (all sites of wet forest); Stainback Highway on the east slope of Mauna Loa at 310 m, 640 m, 940 m, 1220 m, and 1400 m (all sites of wet forest); Strip Road on the south slope of Mauna Loa at 1160 m, 1680 m, and 2000 m (all sites of mesic forest); Manuka on the southwest slope of Mauna Loa at 820 m, 1115 m, and 1430 m (all sites of dry–mesic forest).

Diversity indices for *Tetragnatha* were calculated for each site using the Simpson (S) diversity index, which is sensitive to changes in the most abundant species and so reflects degree of dominance of the most common species:

$$\text{Simpson: } S = 1 - \Sigma p_i^2$$

where S is the Simpson's index of heterogeneity and p_i is the importance probability for each species, $\approx N_i/N_T$.

Interactions of Spiders with Ants

To assess the extent to which spiders might be impacted by two common species of aggressive ants that have been introduced into the Hawaiian Islands, we conducted a series of laboratory experiments. Spiders were collected from native wet and mesic forest between 900 m and 1500 m on the islands of Maui and Molokai and placed singly in covered cages (31 × 16 × 9 cm). Ants were collected from lowland agricultural habitats on Oahu. Colonies of *P. megacephala* were dug out from old pineapple fields and placed in similar cages, but uncovered and with the upper borders painted with teflon to prevent the ants from escaping. *Anoplolepis longipes* were collected individually from rocky stream beds in Manoa Valley, Honolulu, and maintained in cages similar to those of *P. megacephala*. Interactions were conducted in the laboratory at 16°C (the average temperature at 1200 m elevation in Hawaii) by placing spiders in an open container with ants in the following combinations:

(1) Endemic *Tetragnatha* and two species of ants, *A. longipes* and *P. megacephala*. The *Tetragnatha* used in these tests were as follows: (a) web-building species: All of these species build an orb web characteristic of the family Tetragnathidae: *T. stelarobusta* Gillespie, relatively large (average 10.0 mm) with an elongate abdomen; *T. filiciphilia* Gillespie, small (average 5.0 mm) with an oval abdomen; *T. hawaiensis* Simon, large (average 10.8 mm), with an elongate abdomen. (b) non-web-building species: All of these species are cursorial predators and have unusually long spines on the legs: *T. quasimodo* Gillespie, medium-sized (average length 7.7 mm) with a diamond-shaped abdomen; *T. kamakou* Gillespie, medium-sized (average 6.7 mm) with a diamond-shaped abdomen; *T. brevignatha* Gillespie, small (average 5.2 mm) with an oval abdomen.

Four treatments were performed, with five spiders of each species used individually for each interaction with (1) five *P. megacephala* individuals; (2) 25 *P. megacephala* individuals; (3) a colony of *P. megacephala*, composed of 300–400 workers, two to three queens, 30–40 soldiers, and 2–4 ml of brood; (4) 25 *A. longipes* individuals.

(2) Alien spiders and the ant *P. megacephala*. The alien spiders used in these tests were *Araneus* sp. (Araneidae), *Argiope* sp. (Araneidae), *Oxyopes* sp. (Oxyopidae), and *Tetragnatha mandibulata* Walckenaer (Tetragnathidae). Two treatments were performed, with five spiders of each species used individually for each interaction: (1) 25 individual *P. megacephala*; (2) a colony of *P. megacephala*.

Attributes of Spiders Potentially Useful in Defense Against Ants

The aim of this part of the study was to assess whether native *Tetragnatha* are capable of subduing formidable prey, and whether the strategies they use are effective for dealing with dangerous prey, such as predatory ants. For most spiders, wrapping is essential to subdue prey more than $1\frac{1}{2}$ times larger than themselves (Nentwig and Wissel 1986), and such wrapping behavior may allow these spiders to overcome even potentially dangerous prey. We measured the role of silk-wrapping behavior by observing interactions between native *Tetragnatha* and large prey, one to two times the size of the spiders. The prey used were large drosophilids (*Drosophila oahuensis* Hardy, body length ca. 10.0 mm) and calliphorids (*Calliphora* sp., body length ca. 10.5 mm). The *Tetragnatha* used in these tests were *T. stelarobusta*, *T. brevignatha*, and *T. quasimodo*. Five spiders of each species were used for each prey interaction.

RESULTS

Presence of Native Spiders within Habitat Range of Ants in the Hawaiian Islands

The occurrence of ants of different species is compared to the occurrence of native *Tetragnatha* in Figure 1. Except in alien habitats, native spiders were found in most forest (native and disturbed) above 300 m. There were, however, a number of sites of native and

FIGURE 1. Comparison of ranges of ants and endemic *Tetragnatha* spiders in wet and mesic habitats in the Hawaiian Islands. The presence of ants in a given elevational range is indicated by Xs, that of native spiders by Os. Note that a number of species of ants overlap with native spiders. Two species of ants (*Pheidole megacephala* and *Anoplolepis longipes*) occur within the range of native spiders, but never coexist with the spiders, suggesting possible exclusion of the spiders by these species of ants.

X : Range of ants

- X — Range of ants not overlapping that of native spiders
- **X — Range of possible exclusion of spiders by ants**
- X — Range of ants does not overlap that of spiders, but no evidence that this species excludes spiders

O : Range of native spiders
- O — Range of native spiders not overlapping that of ants

XO : Range of overlap
- XO — Ants & native spiders coexist at ≥ 1 site in this range

Elevation (m)	0 - 300	300-600	600-900	900-1200	1200-1500
Cerapachys silvestrii	X	X	O	O	O
Hypoponera punctatissima	X	XO	XO	XO	O
Hypoponera opaciceps	X	XO	XO	XO	O
Ponera swezeyi		XO	O	O	O
Leptogenys falcigera	X	XO	XO	XO	XO
Pheidole fervens	X	X	O	O	O
Pheidole megacephala	X	**X**	**X**	**X**	O
Solenopsis geminata	X	X	O	O	O
Solenopsis papuana	X	XO	XO	XO	O
Monomorium floricola	X	X	O	O	O
Monomorium fossulatum	X	O	O	O	O
Monomorium minutum	X	X	O	O	O
Monomorium pharaonis	X	O	O	O	O
Cardiocondyla emeryi	X	X	X	O	O
Cardiocondyla nuda	X	XO	XO	O	O
Cardiocondyla wroughtoni	X	XO	XO	O	O
Cardiocondyla venustula	X	XO	XO	XO	XO
Tetramorium bicarinatum	X	X	O	O	O
Tetramorium simillimum	X	XO	XO	XO	O
Tetramorium tonganum	X	O	O	O	O
Strumigenys godeffroyi	X	O	O	O	O
Strumigenys rogeri	X	XO	XO	O	O
Quadristruma emmae		X	O	O	O
Iridomyrmex glaber	X	O	O	O	O
Iridomyrmex humilis		O	XO	XO	XO
Tapinoma melanocephalum	X	X	X	O	O
Technomyrmex albipes	X	X	O	O	O
Plagiolepis alluaudi	X	XO	XO	XO	O
Camponotus variegatus	X	X	O	O	O
Anoplolepis longipes	X	**X**	O	O	O
Paratrechina bourbonica	X	XO	XO	XO	XO
Paratrechina vaga	X	XO	XO	XO	O

disturbed forest above 300 m where ants occurred, but no native spiders (indicated by darkest shading in Figure 1). This suggests possible exclusion of the spiders by the ants. In alien habitats, we could not attribute the absence of native spiders directly to exclusion by ants (these areas are unshaded with Xs in Figure 1). The results indicate that native *Tetragnatha* overlap the distributional range of 14 species of ants, *Hypoponera punctatissima* (Roger), *H. opaciceps* (Mayr), *Ponera swezeyi* (Wheeler); *Leptogenys falcigera* Roger, *Solenopsis papuana*, *Cardiocondyla nuda* (Mayr), *C. wroughtoni* (Forel), *C. venustula* Wheeler, *Plagiolepis alluaudi* Emery, *Tetramorium simillimum* (Fr. Smith), *Strumigenys rogeri* Emery, *Iridomyrmex humilis*, *Paratrechina bourbonica* (Forel), and *P. vaga* (Forel). Two species of ants are implicated in the exclusion of spiders from specific sites: *P. megacephala* and *A. longipes*.

Relative Abundance of Ants and Spiders at Specific Sites

The results from the pitfall sampling of ants at specific sites were largely in agreement with the results indicated in Figure 1. We found ants mostly at low elevations (Table 1). *Solenopsis papuana* was often abundant in wet forests and frequently co-occurred with native spiders. *Pheidole megacephala* and *A. longipes* were locally abundant in mesic and dry forests, although native spiders were never found to co-occur with these species.

To test whether *S. papuana* had any effect on *Tetragnatha* abundance, richness, and diversity, we calculated the relationship between the abundance of *S. papuana* (ants per trap per day) where it occurred, and the diversity index, number of species, and abundance of native *Tetragnatha* using regression. The only significant relationship was a negative effect between abundance of ants and the Simpson index of diversity of endemic *Tetragnatha* (Figure 2, $F = 35.71$; df $= 1, 4$; $P = 0.009$). There were insufficient data to determine the relationship between ant abundance and richness and total abundance of endemic *Tetragnatha*.

Interactions of Spiders with Ants

All the interactions between endemic *Tetragnatha* and *P. megacephala* were similar, always resulting in death of the spider (Table 2). (In two cases in which five individual *P. megacephala* were introduced, the ants died before any direct interaction with the spider; these were not included in the analysis.) After various periods of time, an ant grasped the spider with its mandibles. This generally (95% of occurrences; $n = 60$) led to recruitment of other ants, most likely as a consequence of pheromonal release (Wilson 1962). The additional ants initially grasped the spider in the vicinity of the first attack, then other individuals grasped different areas of the body with their mandibles until the spider was pinned down. The number of ants involved in the recruitment phase was highest in the colony interactions (mean, 8.6 ants involved in attack; $n = 30$ trials), with fewer recruits involved when only 5 (mean, 1.8 ants involved in attack; $n = 30$ trials) or 25 ants were used (mean, 2.5 ants involved in attack; $n = 30$ trials). The attack phase lasted from 11 to 240 min (mean, 91.3 min). In a colony interaction the attack phase was shorter (mean, 31.3 min) and spiders were pulled apart, with appendages being carried into the body of the colony by different workers. In interactions with individual ants the attack phase was longer (mean, 113.8 min) and dead spiders were abandoned.

In the interactions between native *Tetragnatha* and *A. longipes*, no recruitment was found. The ants were very active and frequently ran into the spider without attacking it. After various periods of time, however, one ant attacked the spider after running into it. The attack took the form of a rapid wrestle of ca. 2 sec duration, which always resulted in the death of the spider. Death resulted from chemical (formic acid) and/or mechanical (mandibles) damage; the relative importance of these factors could not be ascertained. The ants in this study all abandoned their victims after they had been killed, but it should be noted that we did not use colonies of *A. longipes*. It is likely that the dead spiders

TABLE 1

ANTS AND SPIDERS (*Tetragnatha*) AT DIFFERENT FOREST SITES IN THE HAWAIIAN ISLANDS

SITE	ELEVATION (m)	ANT SPECIES[a]							*Tetragnatha* DIVERSITY INDEX	NO. SPIDER SPECIES	SPIDERS PER HR
		Sp	Pb	Ta	Pm	Pf	Al	Ts			
Low elevation, dry											
Kokee Road, Kauai	610	—	—	—	A	—	—	—	0	0	0
East Manuka, Hawaii	825	—	—	—	—	—	A	P	0	0	0
Mid elevation, dry–mesic											
Waimea Canyon, Kauai	1,040	—	—	—	A	—	—	—	0	0	0
East Manuka, Hawaii	1,115	—	—	—	—	—	N	—	0	0	0
East Manuka, Hawaii	1,430	—	—	—	—	—	—	—	0	0	0
High elevation, dry–mesic											
Mauna Loa Strip Rd., Hawaii	2,000	—	—	—	—	—	—	—	0.3	2	10
Mauna Loa Strip Rd., Hawaii	1,680	—	—	—	—	—	—	—	0	1	56
Low elevation, mesic											
Waianae Kai, Oahu	580	N	—	—	—	—	—	—	0.62	3	20
Mid elevation, mesic											
Kuia N.A.R., Kauai	1,010	—	—	—	—	—	—	—	0.5	3	15
Waimea Canyon, Kauai	1,220	—	—	—	—	—	—	—	0.6	2	
Mauna Loa Strip Rd., Hawaii	1,160	—	—	—	—	—	—	—	0.2	3	32
Low elevation, wet											
Waiahuakua, Kauai	395	—	P	—	—	—	—	P	0.5	2	44
Hanawi, Maui	460	A	—	—	—	—	—	—	0.6	6	28
Kipahulu, Maui	610	N	—	—	—	—	—	—	0.6	4	55
Laupahoehoe, Hawaii	340	—	—	P	—	P	—	—	0	0	0
Stainback Highway, Hawaii	640	N	—	—	—	—	—	—	0.7	4	57
Stainback Highway, Hawaii	310	A	P	—	—	—	—	—	0	0	0
Mid elevation, wet											
Kamakou, Molokai	1,160	—	—	—	—	—	—	—	0.7	7	29
Waikamoi, Maui	1,340	—	—	—	—	—	—	—	0.9	7	46
Kipahulu, Maui	910	—	—	—	—	—	—	—	0.7	7	71
Kipahulu, Maui	1,220	—	—	—	—	—	—	—	0.7	6	61
Laupahoehoe, Hawaii	1,280	—	—	—	—	—	—	—	0.8	7	64
Laupahoehoe, Hawaii	990	—	—	—	—	—	—	—	0.6	7	72
Laupahoehoe, Hawaii	700	—	—	—	—	—	—	—	0.6	6	48
Stainback Highway, Hawaii	1,400	—	—	—	—	—	—	—	0.6	4	63
Stainback Highway, Hawaii	1,220	—	—	—	—	—	—	—	0.8	7	63
Stainback Highway, Hawaii	940	—	—	—	—	—	—	—	0.6	4	60
High elevation, wet											
Honomanu, Maui	1,980	—	—	—	—	—	—	—	0.8	7	42
Kipahulu, Maui	1,525	—	—	—	—	—	—	—	0.8	7	47
Laupahoehoe, Hawaii	1,570	—	—	—	—	—	—	—	0.7	4	20

[a] Sp, *Solenopsis papuana*; Pb, *Paratrechina bourbonica*; Ta, *Technomyrmex albipes*; Pm, *Pheidole megacephala*; Pf, *P. fervens*; Al, *Anoplolepis longipes*; Ts, *Tetramorium simillimum*. A, abundant; N, numerous; P, present; dashes, no ants observed.

would have been carried back into the body of the colony if there were one.

The alien spiders *Araneus* sp. and *Argiope* sp., which were considerably larger than the native *Tetragnatha*, were affected little by interactions with ants. They shook off ants whenever these attempted to bite them, suggesting that their exoskeleton may be less penetrable to attack by ants than that of *Tetragnatha*. The *Oxyopes*, which was similar

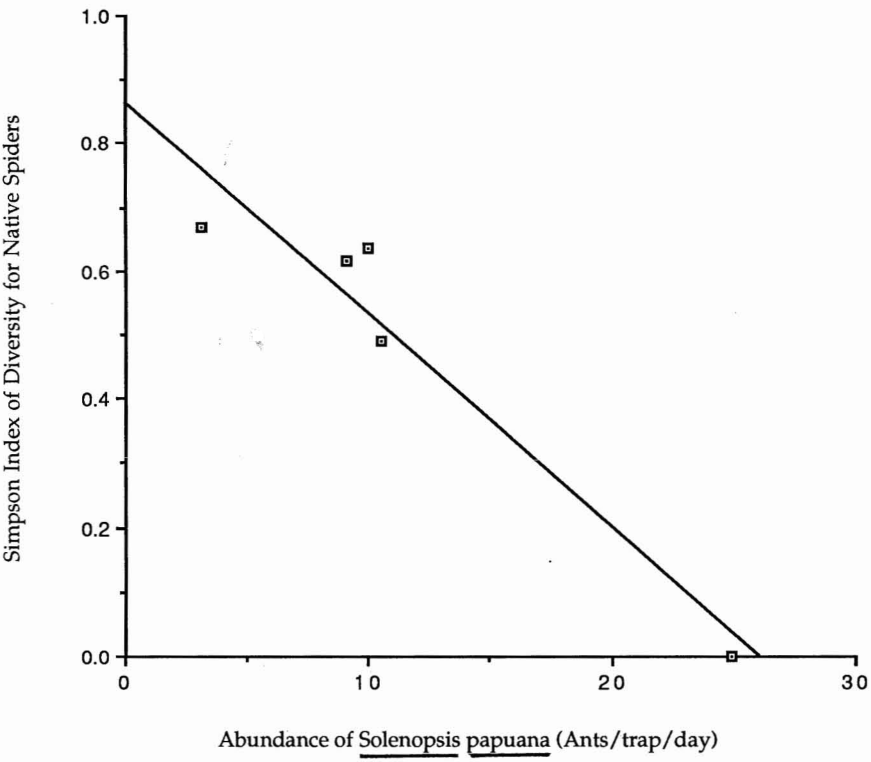

FIGURE 2. Relationship between diversity index of native spiders and abundance of the ant *Solenopsis papuana*.

in size to the native *Tetragnatha*, appendotomized one of its legs in 40% ($n = 10$) of the interactions with *P. megacephala*. This suggests that these spiders may be vulnerable to ant attacks, but appendotomy allows them to escape. The alien tetragnathid *T. mandibulata* was killed by ants in a manner similar to that of the native *Tetragnatha*.

Attributes of Spiders Potentially Useful in Defense Against Ants

Tetragnatha never used immobilization-wrapping to secure prey, even when the prey were >200% the size of the spider, as in the case of *T. brevignatha* and *Calliphora* sp. They grasp the prey in their chelicerae and hold on to it until it is subdued. Both *D. oahuensis* and *Calliphora* sp. were capable of walking around subsequent to having been bitten by *T. brevignatha*, and the spider was carried around with its prey. The only time wrapping was observed, it occurred subsequent to immobilization of the prey.

DISCUSSION

There are six species of common, invasive, predatory ants in the Hawaiian forests: *Solenopsis papuana*, *Paratrechina bourbonica*, *Technomyrmex albipes* (Fr. Smith), *Pheidole megacephala*, *P. fervens* Fr. Smith, *Anoplolepis longipes*, *Tetramorium simillimum*, and *Iridomyrmex humilis*. Our results from native and disturbed forest above 300 m indicate that native spiders occur at most sites, but never those in which either *P. megacephala* or *A. longipes* are present. It is possible that a third variable is responsible for the simultaneous absence of native spiders and presence of *P. megacephala* and/or *A. longipes* at those sites. However, in the absence of any evidence for an additional variable, we suggest that, of all

TABLE 2

INTERACTION OF *Tetragnatha* WITH TWO SPECIES OF ANTS, *Pheidole megacephala* AND *Anoplolepis longipes*

SPIDER SPECIES	*n*	MEAN NUMBER OF ANTS INVOLVED IN ATTACK	ATTACKS RESULTING IN DEATH (%)	ATTACKS RESULTING IN LEG APPENDOTOMY (%)	MEAN TIME TAKEN FOR RESULT (min)
Treatment 1: 5 individuals of *Pheidole megacephala*					
T. filiciphilia	5	2.0	100	—	720.0
T. stelarobusta	5	2.3	100	—	235.7
T. hawaiensis	5	1.7	100	—	411.5
T. brevignatha	5	1.0	100	—	486.0
T. quasimodo	5	2.5	100	—	183.0
T. kamakou	5	1.5	100	—	173.0
Treatment 2: 25 individuals of *Pheidole megacephala*					
T. filiciphilia	5	1.3	100	—	347.0
T. stelarobusta	5	2.3	100	—	123.7
T. hawaiensis	5	1.7	100	—	366.7
T. brevignatha	5	4.0	100	—	118.3
T. quasimodo	5	2.0	100	—	253.3
T. kamakou	5	3.5	100	—	220.0
Argiope sp.	5	—	0	0	—
Oxyopes sp.	5	—	0	0	—
Araneus sp.	5	—	0	0	—
Treatment 3: 25 individuals of *Anoplolepis longipes*					
T. filiciphilia	5	1	100	—	58.0
T. stelarobusta	5	1	100	—	105.2
T. hawaiensis	5	1	100	—	125.5
T. brevignatha	5	1	100	—	35.0
T. quasimodo	5	1	100	—	77.5
T. kamakou	5	1	100	—	98.1
Treatment 4: Colony of *Pheidole megacephala*					
T. filiciphilia	5	8.0	100	—	26.5
T. stelarobusta	5	7.5	100	—	23.0
T. hawaiensis	5	10.5	100	—	66.5
T. brevignatha	5	9.0	100	—	45.0
T. quasimodo	5	10.5	100	—	93.5
T. kamakou	5	6.3	100	—	15.5
Araneus sp.	5	—	0	0	—
Argiope sp.	5	—	0	0	—
Oxyopes sp.	5	2.0	0	40	20.5
T. mandibulata	5	9.5	100	—	82.5

the invasive alien ants in the Islands, *P. megacephala* and *A. longipes* have had the greatest negative impact on native spiders. The suggested negative impact of these ants may be partially attributable to their aggressiveness, coupled with the length of time they have been present in the Islands. *Pheidole megacephala*, the dominant ant throughout the Islands, was first reported in 1899, but was probably present for a considerable time before that date (Huddleston and Fluker 1968). The study reported here shows *P. megacephala* in a wide range of habitats from sea level to 1220 m, and it is frequently abundant in low- and mid-elevation dry-to-mesic forest. *Pheidole fervens* appears to favor wetter habitats, displacing *P. megacephala* in low-elevation wet forest. *Anoplolepis longipes* has expanded its range rapidly since its first collection in 1952 and is now abundant in dry areas (Huddleston and Fluker 1968, Medeiros et al. 1986); it also occurs in low-elevation wet forest on East Maui (Hardy 1979; N.R., pers. obs.).

Solenopsis papuana is also an aggressive species, but although we found a significant negative relationship between ant abundance and spider diversity this species of ant shows extensive range overlap with native spiders, particularly at low elevations. The ability of the spiders to co-occur with the ants may be attributable to the recent invasion of the Hawaiian Islands by *S. papuana*: it was first reported in the Islands in 1967, from Oahu and Hawaii (Huddleston and Fluker 1968). Within a short period, it was found to be widely distributed on Maui and in the Tantalus region of Oahu. It now also occurs on Kauai, Molokai, Lanai, and Hawaii. It may be that the full impact of this species on the native biota has yet to be realized. If we are correct in our consideration of the expanding role of *S. papuana*, this species, the most successful ant to invade native and disturbed wet forest, may be the most serious threat to the native Hawaiian fauna among ant species currently extant in the Islands.

We also found extensive overlap between the native spiders and another apparently aggressive ant species, *I. humilis*, which is known to displace native ants in California (Ward 1987). This species may be gaining inroads into native and disturbed ecosystems in a manner similar to that which we suggest for *S. papuana*, as it has been recorded from a variety of habitats and from sea level to 1830 m (Huddleston and Fluker 1968, Gagné 1979). However, the species has been in the Hawaiian Islands for 50 yr and no longer occurs below 600 m. It is likely that *I. humilis* is only successful above 910 m in the Hawaiian Islands (Fluker and Beardsley 1970). However, there are strong indications that spider numbers have been reduced by *I. humilis* at high elevations (Medeiros et al. 1986).

The 12 species of ants found to co-occur with native spiders in addition to *S. papuana* and *I. humilis* are mostly uncommon, small, and not highly aggressive. The two species of *Hypoponera* are cryptobiotic, inhabiting leaf litter. *Hypoponera opaciceps* is more common than *H. punctatissima* where they co-occur with native spiders, but large populations have never been found, and neither species appears to have had an impact on the native fauna. *Strumigenys rogeri* is another small, cryptobiotic inhabitant of moss and soil. *Leptogenys falcigera* forms small colonies and is uncommon in habitats where it overlaps with Hawaiian *Tetragnatha*. The three species of *Cardiocondyla* all form small, polygynous colonies, are rare where they co-occur with native spiders, and seem to have had little impact on native Hawaiian invertebrates. *Cardiocondyla venustula* is found in a wider range of habitats than *C. nuda* and *C. wroughtoni*, from sea level to 1900 m in dry to wet habitats, but is largely limited to disturbed areas such as agroecosystems and urban developments. *Plagiolepis alluaudi* is rare in habitats where it overlaps with native *Tetragnatha* spiders. *Tetramorium simillimum*, although it may form large, polygynous colonies and occurs from sea level to 1100 m, is limited to locally disturbed sites (e.g., along trails) in habitats where it co-occurs with native spiders. *Paratrechina bourbonica* and *P. vaga* are similarly limited to disturbed sites in areas of co-occurrence.

When pitfall traps were used to assess the relative abundance of ants and spiders at specific sites, some ants were conspicuous by their absence. In particular, we never found *I. humilis*, although it is known to occur at a number of sites in which we sampled. It may be that this species tends not to enter pitfall traps unless baited (Romero and Jaffe 1989).

The laboratory experiments indicated the vulnerability of the spiders to *P. megacephala* and *A. longipes* in the course of direct interaction. How do other spiders tolerate coexistence with ants? The results presented here suggest that both size and the ability to appendotomize appendages may serve as defenses against predation for many continental spiders. In addition, attack strategies in interactions with potentially dangerous prey may also serve a defensive function. Spiders in the family Araneidae may use either "wrap-bite" or "bite-wrap" strategies to deal with large and/or potentially dangerous prey (Nentwig and Wissel 1986), and those in the families Linyphiidae, Theridiidae, Uloboridae, and Agelenidae are also capable of biting and wrapping (Eberhard 1967, Riechert and Luczak 1982). Formidable prey are either wrapped before biting (Robinson and Robinson 1974) or bound in silk while the spider delivers numerous short bites (Riechert and Luczak 1982).

Unlike many families of spiders, Tetragnathidae appear not to make extensive use of silk for the immobilization of formidable prey. The results presented here indicate that the native Hawaiian *Tetragnatha* make no use of silk for prey immobilization, even when the prey is 200% the size of the spider. Similar results have been reported for the Japanese congener, *T. praedonia* L. Koch (Yoshida 1987), which may wrap larger prey when they do not succeed in attack biting, but the silk used is so fine that it cannot be used for immobilization. Studies on other tetragnathid genera indicate that immobilization-wrapping is also absent in *Metleucauge* and incompletely developed in *Leucauge* (Yoshida 1989). On the other hand, the closely related *Meta* has been found to be capable of wrapping ants. The difference in behavior may be because of the insects normally encountered by these genera: *Metleucauge* and *Tetragnatha* outside the Hawaiian Islands build orb webs near or over water and capture primarily small, weak insects emerging from the water. The lack of immobilization-wrapping behavior may result from the absence of large and potentially dangerous prey in such habitats. It may therefore be that the riparian existence of the genus *Tetragnatha* outside the Hawaiian Islands minimizes interaction—and hence possibility of predation—by ants.

In the Hawaiian Islands, the genus *Tetragnatha* is no longer restricted to riparian habitats. Individuals are therefore likely to interact directly with ants introduced into the habitat. The small size of Hawaiian representatives of the genus, coupled with their inability to appendotomize their legs and lack of immobilization-wrapping behavior, may render the native Hawaiian *Tetragnatha* vulnerable to predation, and possible extinction, by aggressive ants such as *P. megacephala*, *A. longipes*, and perhaps also *S. papuana*.

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