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Engineering enemy-free space: an invasive pest that kills its predators

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Abstract

The biological invasion of the glassy-winged sharpshooter, *Homalodisca coagulata*, into French Polynesia presents a novel threat to Pacific Island ecosystems. Widely known as an agricultural pest because of its role as a vector of numerous lethal plant diseases, *H. coagulata* may pose a substantial and immediate risk to arthropod predators on invaded islands in French Polynesia. Controlled feeding experiments revealed that island spiders can be killed following predation on *H. coagulata*. Spider mortality appeared to result from lethal intoxication, although no form of chemical defense has been reported in *H. coagulata*. In the two spider species tested, approximately half of all individuals that attacked *H. coagulata* nymphs or adults died. As populations of this insect increase in size and range on invaded islands in French Polynesia, *H. coagulata* will increasingly encounter these and other arthropod predators, raising the possibility of population-level impacts on susceptible predator species. Field surveys of island spiders across nine sites on *H. coagulata*-invaded and *H. coagulata*-uninvaded islands suggest that this insect may already have adversely impacted an endemic spider on at least one island. Work is needed to identify the nature of the lethal agent harbored within *H. coagulata* and the taxonomic and geographic breadth of predators vulnerable to it. The generality of *H. coagulata*-lethality and the capacity of afflicted predator species for population-level adaptation or learned avoidance in response to this spreading pest will determine the magnitude of the threat *H. coagulata* poses in the South Pacific.

Introduction

The glassy-winged sharpshooter, *Homalodisca coagulata* (Say) (Hemiptera: Cicadellidae), has recently emerged as a devastating invasive insect pest. In California, USA, where *H. coagulata* has been present since the late 1980s (Sorensen and Gill 1996), the threat centers on the role of this xylophage as a vector of the plant pathogenic bacterium *Xylella fastidiosa* (Wells et al. 1987; Hopkins and Purcell 2002). Feeding on over 250 of California's agricultural, ornamental, and native plant species (CDFA 2004), *H. coagulata* has accelerated the spread of endemic *X. fastidiosa* and increased the prevalence of Pierce's disease in vineyards and various "scorching" diseases in almonds, oleander, and liquidambar throughout the insect's invaded range in southern California. This has prompted concern over the fate of the state's premier wine-growing regions should *H. coagulata* continue to spread northwards in California (Hoddle 2004).

In 1999, *Homalodisca coagulata* appeared in French Polynesia (Secretariat of the Pacific Community 2002). Located in the southern Pacific Ocean approximately 5200 km east of Australia and 6000 km west of Chile, the five archipelagos that compose French Polynesia are among the world's most geographically isolated island systems with respect to continental land masses. *Homalodisca coagulata* arrived on Tahiti, the cultural, political, and economic capital of French Polynesia's 118 islands in 1999, and had spread to neighboring Mo'orea by 2002 (Secretariat of the Pacific Community 2002). Today, extremely large *H. coagulata* populations are readily found feeding and reproducing on a variety of exotic and native plants in urban areas on these two islands, and while less abundant at higher elevations, individuals can be found even in undisturbed native habitat on volcanic peaks up to 900 m above sea level (K.B. Suttle, personal observation). In French Polyneisa, growing public concern over this newly arrived pest does not owe solely to plant disease. *Homalodisca coagulata* populations on Tahiti and Mo'orea have grown to levels far exceeding California or its native range in the southeastern USA and northeastern Mexico. Consequently, the copious excreta that "rains" from infested trees has become a common nuisance, earning *H. coagulata* the local name *meuche pisseuse* ("urinating fly"). It is unknown whether the pathogenic bacterium *X. fastidiosa* exists in French Polynesia, having been accidentally imported within symptomless ornamental plants from the Americas, but to date no leaf scorching indicative of disease has been observed. This could be due to the long length of time required for manifestation of symptoms following successful infection, especially for large woody trees and shrubs (Purcell 1997). Should *X. fastidiosa* appear in French Polynesia, it will likely threaten many native plant species due to the extreme polyphagy of *H. coagulata*, as this vector challenges novel host species that have no evolutionary association with *X. fastidiosa* by inoculating them with the bacteria. We report here, however, that upper trophic level organisms in French Polynesia are at more immediate risk from *H. coagulata* than susceptible plant species that could potentially die from *X. fastidiosa* infection.

As *H. coagulata* populations increase in abundance and range on invaded islands, the insect comes into contact with numerous generalist invertebrate arboreal predators. Jumping spiders (Araneae: Salticidae) are common in vegetation on which *H. coagulata* feeds and reproduces throughout its invaded range. Large communal web complexes of the orb-weaving spider *Cyrtophora moluccensis* (Araneae: Araneidae) are likely to ensnare winged adult *H. coagulata* as the insect spreads into mid-elevation (100–400 m) forests. And as *H. coagulata* ultimately establishes breeding populations in higher-elevation, interior forest patches, it will increasingly encounter the native crab spider, *Misumenops melloleitao* (Araneae: Thomisidae) (Figure 1), which hunts on the leaves, branches, and flowers of several montane trees and shrubs.

We have discovered through feeding trials with spiders collected from Tahiti and Mo'orea that *H. coagulata* can lethally intoxicate or repel invertebrate predators that attack and attempt to feed on nymphs or adults. The presence of what is assumed to be a chemical defense is surprising given that this insect is thought to feed exclusively on xylem fluids, which lack defensive secondary chemicals that can be sequestered by consumers (Raven 1983). Such adverse effects on predators have not been observed previously in the native range of *H. coagulata* or the recently invaded mainland range of California. This novel consequence to biological invasion presents a unique threat to island spiders. And because direct lethal effects on spiders could have myriad indirect effects on the predators, competitors, and prey of those spiders, *H. coagulata* could pervasively alter the structure and species composition of island food webs. Here we document the lethality of *H. coagulata* observed in controlled, replicated feeding trials with two spider species in French Polynesia. We then extrapolate the results of these feeding trials to potential field-level impacts of *H. coagulata* on spider populations based on field surveys of native crab spider abundance on invaded and uninvaded islands.

Materials and methods

Feeding trials with French Polynesian spiders

Feeding trials between *H. coagulata* and two species of island spiders, *M. melloleitao* (Araneae: Thomisidae) and *C. moluccensis* (Araneae:

Figure 1. Predation attempt by the crab spider, *M. melloleitao*, on *H. coagulata.*

Araneidae), were conducted on Mo'orea and Tahiti in October 2003 and May 2004 (Table 1). *Homalodisca coagulata* nymphs and adults used in these trials were collected on these two islands both from ornamental plant species at coastal sites and from native and exotic vegetation at interior sites.

Endemic to the Society Islands, *M. melloleitao* is restricted to higher elevations (300–1200 m) and found predominantly on montane trees and shrubs (Gillespie et al. 2000). This species was collected by sweep-netting vegetation on Mt. Mouaputa on Mo'orea and Mts. Marau and Teatara on Tahiti, and housed individually in 30 ml plastic containers for feeding trials. Trials with *M. melloleitao* began with the random assignment to each spider of one of two prey types, an *H. coagulata* nymph or a comparably sized fly (*Drosophila* or *Musca* spp.). A single motile *H. coagulata* nymph (2nd to 4th instar) or

Table 1. The results of feeding trials conducted on Mo'orea and Tahiti.[a]

Date	Species	Prey	*N*	Attack rate (%)	Mortality rate (%)
2003	*M. melloleitao*	GWSS	30	100	43
2003	*M. melloleitao*	Control	12	100	0
2004	*M. melloleitao*	GWSS	15	67	60
2004	*M. melloleitao*	Control	8	100	0
2003	*C. moluccensis*	GWSS	10	100	70
2003	*C. moluccensis*	Control	10	100	0
2004	*C. moluccensis*	GWSS	10	100	60

[a] Spiders were offered either a single *H. coagulata* or a comparably sized fly, as a control. *Crtophora moluccensis* was not fed control prey in 2004 feeding trials; colonies of this spider species were extremely rare at the time studies were conducted, and a previous detailed study of their feeding habits revealed no ill effects of consumption of non-*H. coagulata* prey (Y. Stone, unpublished data).

fly was then introduced into each spider's container. The specific age class of *H. coagulata* presented depended on the size of each spider; prey were selected to be smaller than or approximately equal in size to corresponding spiders (*M. melloleitao* size range 0.0031–0.0304 g; *H. coagulata* 0.0025–0.0184 g).

The communal orb-web spider, *C. moluccensis*, is distributed widely across the Indian and Pacific Oceans, and is known from India and Japan to Australia and east into the Pacific (Platnick 2004). In the Society Islands, it occurs predominantly in forest understory habitats. Feeding trials with *C. moluccensis* were performed in the field on Mo'orea at two communal web complexes constructed by this species. In October 2003, trials began with the random designation to each experimental spider of a single glassy-winged sharpshooter or a comparably sized fly. Adult *H. coagulata* were used in most feeding trials, as this winged stage is the most likely to encounter *C. moluccensis* under natural circumstances. Prey were thrown by hand directly into the individual orb web occupied by each experimental spider in the larger complex.

In trials with both spider species, the timing of all interactions between spider and insect (e.g., attack, consumption, discard) and any spider responses was recorded on a stopwatch from the moment of prey introduction. Consumption time was defined as the period in which prey were held in the chelicerae. Each spider was observed continuously for three hours following prey capture. All spiders that survived beyond this three-hour observation period were then monitored daily for survivorship over three consecutive days.

Field surveys of Misumenops *spp.*

In October and November 2003 and May and June 2004, we visited nine interior montane sites distributed across four islands in the Society Islands and Marquesas Islands archipelagos (Table 2). Populations of endemic crab spiders (*M. melloleitao* in the Society Islands and *Misumenops delmasi* in the Marquesas) had been recorded at each of these sites in government-sponsored surveys conducted in 2000 (Gillespie et al. 2000). Since the completion of those surveys, *H. coagulata* has flourished on Tahiti and Mo'orea. We revisited each site to monitor crab spider abundance and presence/absence of *H. coagulata*. In the original surveys, *M. melloleitao* and *M. delmasi* had been collected by sweep-netting and beating branches of the montane forest species *Metrosideros collina, Inocarpus fagifer, Cyathea spp*, and *Dicranopteris sp.* (Gillespie et al. 2000). We employed similar sampling protocols to re-sample this vegetation at each site, adding to the sample the native tree *Weinmannia parviflora*, from which we had collected *M. melloleitao* in preliminary work on Tahiti. Lower-lying vegetation (<2.5 m aboveground) was sampled with sweep-nets (38 cm diameter). Higher-lying vegetation (up to 4 m aboveground) was sampled by beating branches with a telescoping pole over a bed sheet spread below (~5 m^2 capture area on the ground below the branches being sampled). We drew catch-per-unit-effort measures of crab spider abundance on this vegetation at each site, defined as the number of individual *M. melloleitao* and *M. delmasi* collected per hour of sampling effort.

Table 2. Results from surveys of *M. melloleitao* abundance at nine sites at which this species was documented in 2000.

Island	Site	Samples	Mean catch/hour	*H. coagulata*
Mo'orea	Belvedere	4	0	Yes
Mo'orea	Vaiare-PaoPao	4	0	Yes
Mo'orea	Mt. Mouaputa	3	3.83	Yes
Tahiti	Belvedere	2	4.83	Yes
Tahiti	Marau	2	5.75	No
Ra'iatea	Temihani	1	1.5	No
Nuku Hiva	Mt. Muake	1	3	No
Nuku Hiva	Muake-Taiohae	1	3	No
Nuku Hiva	Tovii	1	3.5	No

The specific selection of sampled vegetation varied across sites due to limitations imposed by the terrain. The majority of sampling sites (i.e., Mt. Marau and Belvedere on Tahiti, Belvedere on Mo'orea, Temihani Plateau on Ra'iatea, Muake-Taiohae Trail and Tovii Plateau on Nuku Hiva) afforded sufficiently accessible terrain to allow extensive sampling of vegetation. At these sites, we sampled as many representatives of each plant species on which *M. melloleitao* is known to occur as could be located and accessed in a sampling period of 2–4 h. In addition, we spent 30–60 min sampling non-target plant species at each of these sites. Other sites (i.e., Mt. Mouaputa and Vaiare-PaoPao summit on Mo'orea, Mt. Muake on Nuku Hiva) on steep volcanic peaks or ridges were accessible only by narrow trails, with the terrain dropping sharply on either side. With little access to off-trail vegetation, available vegetation could be sampled with one to three hours of sampling effort. After no *Misumenops spp.* were found during the first visits to the Mo'orea Belvedere and Vaiare-PaoPao summit sites in October 2003, those sites were resurveyed twice that autumn at 10–15 day intervals and again the following May.

Results

Feeding trials with French Polynesian spiders

Misumenops melloleitao attacked and consumed all presented prey in October 2003. Forty-three percent of these spiders (13/30) died within 1 h of initial attack and feeding on a single *H. coagulata* nymph (Table 1). In the paired controls, spiders exhibited no discernible changes in behavior or vitality during the same observation interval following predation on *Drosophila and Musca* spp. In May 2004, the attack rate on *Drosophila* remained at 100%, but 5 out of 15 spiders approached *H. coagulata* nymphs and retreated without initiating any physical contact. Of the 10 crab spiders that did attack and feed on *H. coagulata*, 6 died within 1 h of attack (Table 1). Again, consumption of *Drosophila* elicited no change in the behavior or vitality of control group spiders. In both sets of feeding trials, the average consumption period of *M. melloleitao* on *H. coagulata* was less than 15% the feeding period on control prey (2003, $t_{40} = 10.8$, $P < 0.001$; 2004, $t_{16} = 7.9$, $P < 0.001$) (Figure 2).

The orb-weaving *C. moluccensis* attacked and consumed all presented prey in the October 2003 and May 2004 field-based feeding trials. Of 10 *C. moluccensis* that consumed *H. coagulata* in October 2003, 8 entered an unresponsive state while feeding on or within minutes of discarding the prey. These spiders became lethargic and non-responsive to tappings on their web silks and puffs of air blown directly on them. This unresponsiveness contrasted from the pronounced defensive behaviors exhibited by two other *C. moluccensis* consuming *H. coagulata*, the 10 control spiders feeding on flies, and other colony members not included in feeding trials. The eight spiders that entered this intoxicated state lost contact between several legs and the web structure. Hanging asymmetrically below their feeding platforms, two *C. moluccensis* died with *H. coagulata* prey still embedded in their chelicerae. The other six spiders discarded their prey and secreted an unidentified amber fluid from their mouthparts (Figure 3) for the next 1–3 h. Five of these spiders died following exudation of fluids, either dropping to the ground beneath the web complex or becoming entangled in web silks while in a lethargic state; thus seven of ten *C. moluccensis* that attacked and consumed *H. coagulata* died in the encounter (Table 1). One spider recovered from this intoxicated state

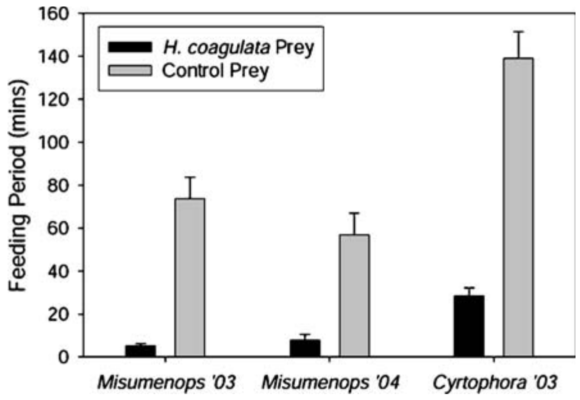

Figure 2. The duration of consumption by spider predators on *H. coagulata* and on comparably sized flies (*Drosophila and Musca* spp.). Data represent mean values plus standard errors across all feeding trials ($n = 95$).

Figure 3. An intoxicated *C. moluccensis*, following predation on an adult *H. coagulata*. The spider has lost contact between several legs and its web structure and is secreting an unidentified amber fluid from its fangs.

after approximately two hours, its subsequent defensive behavior not discernibly different from the two *C. moluccensis* that exhibited no negative response to predation on *H. coagulata* or from others in the colony that had not fed on *H. coagulata*. After consuming flies, *C. moluccensis* exhibited no discernible change in vitality or defensive behavior. Overall, average consumption time by this species on *H. coagulata* was less than 25% the duration of feeding on flies (t_{28}, = 11.5, $P < 0.001$) (Figure 2).

In May 2004, 6 of 10 *C. moluccensis* died after predation on *H. coagulata* (Table 1). Of the four spiders that survived consumption of *H. coagulata*, two entered into and later emerged from an intoxicated state as described above, while another two never exhibited a discernible negative response to feeding on *H. coagulata*. In the May 2004 feeding trials, *C. moluccensis* that survived consumption of *H. coagulata* were presented with subsequent *H. coagulata* adults on the following day. These four spiders quickly (< 8 s) and consistently rejected this prey, either during orientation and approach to the entangled insect or after initial inspection of prey with pedipalps.

In neither spider species did mortality correlate with increased consumption time on *H. coagulata* (Figure 4). *Misumenops melloleitao* that survived predation on *H. coagulata* fed for a roughly equal period to those that died (Logistic Regression $n = 40$, $P = 0.88$). In *C. moluccensis*, there was a nearly significant correlation between the incidence of mortality and lower consumption time ($n = 20$, $P = 0.06$).

Field surveys of Misumenops spp.

Endemic crab spider (*Misumenops spp.*) populations were documented at numerous sites across the Society Islands and Marquesas Islands archipelagos in the year after *H. coagulata* was first detected on Tahiti (Gillespie et al. 2000). Since the completion of those surveys, *H. coagulata* has become abundant on Tahiti and neighboring Mo'orea. Results from surveys conducted as part of this study indicated that on Tahiti, *H. coagulata* adults and nymphs are seasonally abundant around Belvedere (elevation 650 m), but either absent from or at undetectable densities in the summit regions of Mt. Marau

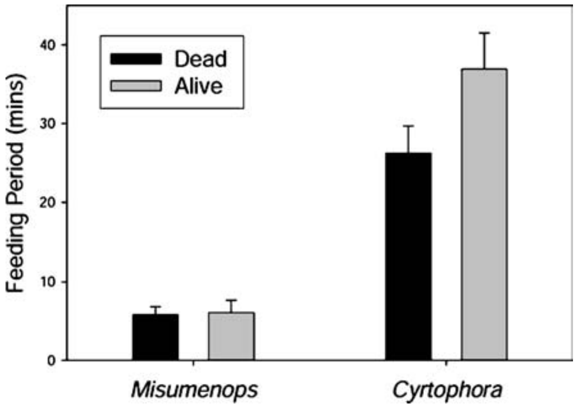

Figure 4. The duration of consumption of *H. coagulata* by spider predators that survived the encounter (Alive) and those that perished (Dead).

(elevation 1493 m). On Mo'orea, *H. coagulata* is common around the Belvedere and Vaiare-PaoPao summit sites (elevation 550 and 325 m, respectively), and present in lower abundances on Mt. Mouaputa (elevation 830 m). *Homalodisca coagulata* is not known to occur on Mt. Temihani on Ra'iatea or on the island of Nuku Hiva (Table 2).

We readily collected *M. melloleitao* at all but two survey sites in the Society Islands, and we collected *M. delmasi* without difficulty at all three sites on Nuku Hiva in the Marquesas Islands (Table 2). We were unable to collect *M. melloleitao* from the Belvedere and Vaiare-PaoPao summit sites on Mo'orea. We made three sampling visits to each of these sites in autumn 2003 and conducted an additional survey in spring 2004, but failed to collect a single *M. melloleitao* at either site. This species had been readily collected at both of these sites by scientists two years prior to the arrival of *H. coagulata* on Mo'orea (Gillespie et al. 2000).

Discussion

Biological invasions are at the forefront of ecological research, both for the insight they can provide about the structure and organization of invaded systems and because of their demonstrated potential to inflict economic and ecological damage upon recipient ecosystems. A major problem associated with the invasion and spread of exotic organisms is the displacement of native species through the introduction of disease or disruption of ecosystem processes, trophic relationships, and competitive hierarchies. The severity of these impacts can often be explained by the population densities attained by invasive organisms: many organisms flourish in their invaded ranges in far greater abundances than in native ranges (Louda et al. 1990; Mack et al. 2000). Much of the damage caused by aquatic and terrestrial invertebrates and plants in exotic ranges has been a direct result of the high densities they attain (e.g., Johnson and Carlton 1996; Porter et al. 1997; Holway et al. 1998; Sheley et al. 1998; Strayer et al. 1998; Ridenour and Callaway 2001; Vivanco et al. 2004).

A leading explanation for the disproportionate success enjoyed by many exotic organisms in invaded relative to native ranges is escape from coevolved natural enemies (Darwin 1859; Elton 1958; Lodge 1993; Mack et al. 2000; Keane and Crawley 2002; Levine et al. 2002; Mitchell and Power 2003; Torchin et al. 2003). According to the "natural enemies" (or enemy-release) hypothesis, organisms that arrive in new habitats free from the complement of predators, parasites, and pathogens that limit population growth in their native ranges may flourish unchecked where competition for resources is slight and climate is favorable. Classical biological control efforts often involve the deliberate introduction of co-evolved, specialized enemies from the organism's native range into its invaded range – this is the case in California, where parasitoids (Hymenoptera: Mymaridae) that attack *H. coagulata* eggs have been imported from southeastern USA and northeastern Mexico for release against *H. coagulata* (Vickerman et al. 2004).

A recent alternative to the natural enemies hypothesis posits that certain organisms thrive in exotic ranges through the use of allelochemicals that function as "novel weapons" against native competitors that lack an evolutionary history with these compounds (Callaway and Aschehoug 2000; Bais et al. 2003; Callaway and Ridenour 2004; Vivanco et al. 2004). In French Polynesia, *H. coagulata* appears to benefit from a combination of invasion strategies. The absence of specialist natural enemies such as parasitoids on invaded islands combined with the killing of ecologically naïve generalist predators may explain the extraordinary invasion success of *H. coagulata* on Tahiti and Mo'orea.

In the five years since its introduction to French Polynesia, *H. coagulata* may already have impacted *M. melloleitao* populations on Mo'orea. Our failure to detect any *M. melloleitao* at two sites at which this spider was known to occur in 2000 could reflect differences in our collection techniques relative to those employed by Gillespie et al. (2000) or declines in *M. melloleitao* abundance at these sites since 2000. To assess the likelihood of either possibility, we re-sampled multiple sites at which Gillespie and colleagues had documented native crab spider populations in 2000 (Table 2), intuiting that consistently lower collection levels across sites relative to those earlier surveys would suggest discrepancies in sampling protocol, while anomalously low collection levels at select sites might point instead toward lower abundances of *M. melloleitao* in those regions.

We collected native *Misumenops* spiders at every other accessible site from the 2000 surveys. The two sites at which we were unable to document *M. melloleitao* are both regions in which *H. coagulata* has become abundant since the earlier surveys. Our failure to detect *M. melloleitao* at these two sites does not necessarily indicate an absence of this species; indeed, a single individual was collected in a later survey at the Mo'orea Belvedere site by another researcher (G. Roderick, personal communication). It is likely, however, that *M. melloleitao* has declined in response to an abundant and deadly prey organism which it is poorly adapted to use as food.

Homalodisca coagulata is extraordinary for the variety of ways in which it can impact an invaded ecosystem. Threats posed by this insect span up and down the food web, from the plants on which it feeds and native hemiptera with which it may compete to the predators that attack it. And indirect effects of *H. coagulata* invasion may be pervasive, as direct lethal effects on spiders impact the predators, competitors, and particularly the prey of those spiders. By killing generalist predators, *H. coagulata* may create enemy-free space (Jeffries and Lawton 1984) not just for itself, but for other insects as well. This indirect benefit to alternate prey species is analogous, though opposite in sign, to apparent competition, where support of a shared enemy indirectly harms alternate prey of that enemy (Holt 1984, Holt and Lawton 1993). One further step along this hypothetical interaction chain reveals the diverse pathways by which *H. coagulata* can damage the flora of invaded islands. In addition to direct feeding from the xylem of host plants, which can inflict or exacerbate water stress, and transmission of *X. fastidiosa*, which can kill plants outright, *H. coagulata* may increase plant tissue damage by relieving predation pressure on herbivorous insects. The likelihood of such indirect effects will come more clearly into focus when we determine the actual taxonomic breadth of predator species that can be killed by feeding on the glassy-winged sharpshooter and the population-level consequences of this surprising interaction for these predators.

The nature of chemical protection in *H. coagulata*, should it be responsible for spider mortality, is unclear, but it is unlikely that lethal compounds are simply sequestered from plants upon which the insect feeds. Not only does *H. coagulata* feed on xylem fluids, which generally lack defensive secondary chemicals (Raven 1983), but we found that the lethality of sharpshooters did not vary with host plant origin. *Homalodisca coagulata* nymphs and adults used in the feeding trials were collected from interior vegetation and coastal ornamental plant species. Having no wings, nymphs most likely develop on or near the plant from which they hatch. It is unlikely that nymphs collected from interior vegetation could also have fed on coastal ornamental plants, or vice versa. It is possible, therefore, that lethal compounds are manufactured *de novo*.

We speculate that bacterial endosymbionts (a-symbionts and t-symbionts) present in *H. coagulata* bacteriomes could be responsible for the toxic effect on *M. melloleitao* and *C. moluccensis*. Obligate bacterial mutualists are thought to mitigate nutritional deficiencies for their host that result from the low nutritional value of xylem fluids (Moran et al. 2003). It is possible that these bacteria in bacteriomes provide not only nutrition, but also chemical protection for the host, either by modifying ingested xylem compounds or through the creation of unique bacterial compounds that are toxic. Alternatively, the plant pathogenic *X. fastidiosa* may afford chemical protection to *H. coagulata*, thereby ensuring its own survival and transmission within its vector. It is unknown whether *X. fastidiosa* is present in French Polynesia, as comprehensive surveys for this bacterium have yet to be conducted. If *X. fastidiosa* is responsible for mediating biochemical protection of *H. coagulata*, then the fact that some spiders survive predation events may reflect the absence of this bacterium in some hosts, as it is not an obligate symbiont of *H. coagulata* and can be obtained only by feeding on infected plants. *Xylella fastidiosa* is lost from the mouthparts each time *H. coagulata* nymphs molt, and must be reacquired by feeding on infected host plants. Interestingly, genome sequencing of *X. fastidiosa* has identified gene sequences responsible for the production of proteins that confer pathogenicity to human and animal pathogens (Simpson et al. 2000). Moreover, a defensive role for microbial endosymbionts in the hemiptera is not without precedent. Scientists working with the pea aphid, *Acyrthosiphon pisum*, have recently demonstrated that facultative bacterial symbionts harbored in this insect mediate protection against *A. pisum*'s most important natural enemy, the hymenopteran parasitoid, *Aphidius ervi* (Oliver et al. 2003). Although the mechanisms underlying this interaction have not been resolved, the defensive role of these bacterial mutualists is reflected in increased mortality of developing wasp larvae inside the body cavities of infected living aphids relative to uninfected controls.

Mechanisms underlying the survival of 28 out of 60 individual spiders in our feeding trials with *H. coagulata* are also poorly understood. Assuming toxicity in *H. coagulata* is indeed responsible for spider mortality and the toxin is always present in *H. coagulata*, it does not appear to operate in a dosage-dependent manner. In *M. melloleitao*, the incidence of mortality did not correlate with increased consumption time on *H. coagulata*, and in *C. moluccensis* there was actually a trend toward longer feeding periods in spiders that survived predation on *H. coagulata* (Figure 4). Survival may instead have been based on some aspect of spider quality (e.g., diet history, nutritional state, age, time since last molt, etc.) at the time of predation on *H. coagulata* or on genetic differences in susceptibility among individual spiders in each population. Support for the role of nutritional state is provided by comparing the initial observations that led to the experiments described here with the results of those experiments. We began controlled feeding trials after observing mortality in nine of nine *M. melloleitao* immediately following predation on *H. coagulata* nymphs. All nine of these spiders had been deprived of food for seven to ten days prior to this feeding. The controlled laboratory feeding trials described in this report (in which we observed 47% mortality in *M. melloleitao*) were conducted within three days of collecting these spiders from the field. We did not standardize diet in any experimental spiders prior to feeding trials, leaving open the possibility of a wide range of nutritional states or time-since-last-predation events in these test individuals.

Identifying the mechanisms underlying individual response to predation on *H. coagulata* may be fundamental to predicting the fate of afflicted predator species. If survival of individual spiders is based on some aspect of spider quality, then *H. coagulata*-imposed mortality should impact each new generation. A species' capacity for learned avoidance following non-lethal encounters will influence its population-level response to *H. coagulata*. The observation that 5 out of 15 *M. melloleitao* refused *H. coagulata* outright during May 2004 feeding trials after a 100% attack rate in the October 2003 trials is suggestive of learned avoidance. All *M. melloleitao* used in our research were collected from areas in which *H. coagulata* is known to exist. The six-month period between feeding trials allows for the possibility that a naïve spider population in 2003 gained experience through increased encounters with *H. coagulata* as *H. coagulata* densities and geographic distribution increased. These issues can be resolved through research with spiders reared in a controlled environment, which will allow for standardization of aspects of spider quality that could influence vulnerability to *H. coagulata* intoxication.

If survival is based instead on genetic differences within each spider population, then afflicted spider populations may undergo strong genetic selection and rapid adaptation in response to this severe selective pressure, their persistence contingent on surviving population bottlenecks that follow the die-off of susceptible individuals. This process may ultimately replicate itself on islands across the South Pacific if *H. coagulata* spread continues (large populations of *H. coagulata* were detected in Hawaii in 2004 – (Heu et al. 2004)). Quarantine measures are in place in French Polynesia to retard the spread of *H. coagulata* to neighboring South Pacific islands, but preventing further introductions and colonizations will be difficult. Female *H. coagulata* deposit eggs beneath the epidermis on the undersides of leaves of nearly 200 plant species in California (CDFA 2004) and at least 100 species on Tahiti and Mo'orea (L. Parnell, personal communication). As trade, travel, and tourism between the islands of French Polynesia and the rest of the world continue, so may the inadvertent transport of *H. coagulata* (Hoddle 2004) and its subsequent impact on fragile island ecosystems.

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