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ZELUS RENARDII AND *Z. TETRACANTHUS* (HEMIPTERA: REDUVIIDAE): BIOLOGICAL ATTRIBUTES AND THE POTENTIAL FOR DISPERSAL IN TWO ASSASSIN BUG SPECIES

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Abstract

The leafhopper assassin bug, *Zelus renardii* Kolenati, is a natural enemy and stands out among species in the large New World genus *Zelus* Fabricius (~60 spp.) by its introduction to and establishment in 3 biogeographic regions. We here present documentation of the distribution and habitat of *Z. renardii* in its native range in North and Central America and compare it with *Z. tetracanthus* Stål, a wide-ranging New World congener that apparently has not dispersed outside of its native range. In addition, we document and compare predatory and reproductive behaviors in the 2 species. *Zelus renardii* is widely distributed in the Western USA and shows a continuous geographic range south to Guatemala; *Z. tetracanthus* is broadly distributed across North and Central America and also occurs in Brazil. In Riverside County, California, *Z. renardii* is common in suburban and disturbed habitats in addition to certain natural areas, whereas *Z. tetracanthus* is usually restricted to natural areas. The behavioral comparison under laboratory conditions indicated that *Z. renardii* caught prey faster and that feeding duration in this species was shorter than in *Z. tetracanthus*. The duration of pre-copulatory behaviors in *Z. renardii* was shorter than in *Z. tetracanthus*, resulting in a shorter overall mating duration. Based on the higher percentage of egg batches that produced first instars in *Z. renardii*, this species may establish large populations under adverse conditions faster than *Z. tetracanthus*. Our observations on distribution and biology contribute toward an understanding of the differences in invasiveness between the 2 species.

Key Words: adverse conditions, assassin bug, differential dispersal, distribution, mating, pioneer species, predation

Resumen

La chinche asesina, *Zelus renardii* Kolenati, es un enemigo natural y se destaca entre las especies del gran género del Nuevo Mundo *Zelus* Fabricius (~60 spp.) por su introducción y establecimiento en tres regiones biogeográficas. Presentamos documentación sobre la distribución y el hábitat de *Z. renardii* en su área de distribución nativa en Norte y Centroamérica, y la comparamos con *Z. tetracanthus* Stål, un congénere de amplia distribución en el Nuevo Mundo que al parecer no es dispersalista. Adicionalmente, documentamos y comparamos comportamientos predadoresy reproductivos en las dos especies. *Zelus renardii* se encuentra ampliamente distribuido en el oeste de los EE.UU. y muestra un rango geográfico continuo hasta el sur de Guatemala; *Z. tetracanthus* está ampliamente distribuida a través de Norte y Centroamérica, y también esta presente en Brasil. En el condado de Riverside, California, *Z. renardii* es común en hábitats perturbados y suburbanos además de ciertas áreas naturales, mientras que *Z. tetracanthus* suele estar restringida a áreas naturales. La comparación del comportamiento bajo condiciones de laboratorio indicó que *Z. renardii* capturaba presas más rápido y que la duración de la alimentación en esta especie era más corta que en *Z. tetracanthus*. La duración de comportamientos precopulatorios en *Z. renardii* fue más corta que en *Z. tetracanthus* resultando en una duración más corta de apareamiento. Con base en el porcentaje más alto de lotes de huevos que produjeron ninfas de primer estadío en *Z. renardii*, esta especie puede establecer poblaciones grandes en condiciones adversas más rápido que *Z. tetracanthus*. Nuestras observaciones sobre la distribución y biología entre las dos especies contribuyen a la comprensión de las diferencias en su potencial invasivo.

Palabras Clave: condiciones adversas, chinche asesina, dispersión diferencial, distribución, cópula, especie pionera, depredación

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All but one species of the assassin bug genus *Zelus* Fabricius (Hemiptera: Reduviidae) (~60 spp.) are restricted to the New World where they are roughly distributed between Argentina and Canada, including the Caribbean (Maldonado 1990; Hart 1972; 1986, 1987). An exception is the leafhopper assassin bug, *Zelus renardii* Kolenati, that as early as 1897 was not only recorded from its native range, mainland North and Central America, but was also reported to have invaded the tropical areas of Hawaii (Kirkaldy 1903, 1910; Zimmermann 1948; Wygodzinsky 1966) where it was found to feed on the invasive sugarcane leafhopper, *Perkinsiella saccharicida* Kirkaldy, 1903 (Hemiptera: Delphacidae), among other arthropod prey species. Hart (1986) reported *Z. renardii* from additional tropical areas in the Pacific Region, i.e., Johnston Island (North Pacific), Samoa (South Pacific), and the Philippines. Starting in 2001, *Z. renardii* was reported from Chile (Curkovik et al. 2004; Elgueta & Carpintero 2004 [incorrectly identified as *Zelus cervicalis* Stål in the latter, as confirmed by one of the authors {GY}]), where it was found in 3 neighboring regions, O'Higgins, Valparaíso, and the Santiago Metropolitan Region, spanning latitudes of 33° to 35°S that are primarily characterized by a Mediterranean type climate. As of 2010, *Z. renardii* was also recorded from the Mediterranean region in Europe, specifically Greece (Davranoglou 2011) and Spain (Klaus Kamppeter, personal communication).

Zelus spp. prey on a wide range of insects in cotton, soybean, alfalfa, and fruit trees (Ali & Watson 1978; Cisneros & Rosenheim 1998) and were in one instance reported to have reached population densities of 50,000 to 75,000/ha in one location in Texas (Ables 1978). Certain aspects of the ecology, behavior, and physiology of different species of *Zelus* have accordingly been examined in the context of their potential as natural enemies. Early studies described the predatory behavior of *Zelus luridus* Stål (Edwards 1966) and mating and predatory behaviors as well as the immature stages of *Z. tetracanthus* (Swadener & Yonke 1973). Subsequently, the influence of prey size to predation success was investigated experimentally in *Z. renardii* and *Zelus longipes* Linné (Cohen & Tang 1997; Cogni et al. 2002) and the enzyme composition of the saliva of *Z. renardii* was characterized (Cohen 1993). The unique predation technique involving sticky substances secreted by dermal glands in species of *Zelus* was the subject of several studies (Wolf & Reid 2001; Weirauch 2006; Zhang & Weirauch 2012). These sticky glands are absent in early instars. Instead, first instars use sticky secretions that females deposit on their egg mass (Weirauch 2006). Law & Sediqi (2010) showed that, in *Z. renardii*, this sticky substance increases predation success and enhances the bug's adherence to the substrate.

Despite previous research, distributional, ecological, and behavioral observations are lacking that may help to explain why *Z. renardii* has established outside its native range, but other *Zelus* species have not. We propose 3 hypotheses that may explain this phenomenon: *Zelus renardii* may have a large distribution range across various climatic zones, but other *Zelus* spp. may have more restricted geographic distributions and climatic preferences. *Zelus renardii* may therefore be more likely to be successful under environmentally diverse circumstances. The second hypothesis involves the relative proximity of different species of *Zelus* to humans: *Zelus renardii* has likely reached Hawaii, Chile, and the Mediterranean by human-assisted introductions. Does *Z. renardii* show greater abundances in disturbed environments, including agricultural and urban landscapes, than other species of *Zelus*? Greater proximity to humans could facilitate transport of *Z. renardii* individuals through commerce, e.g. in nursery stock. Finally, basic biological parameters, such as predation efficiency and mating duration, may also be involved in the apparent dispersalist success of *Z. renardii* over other species of *Zelus.* Despite previous studies on predatory and reproductive behaviors for several species of *Zelus*, no study has documented these behaviors in direct comparison of *Z. renardii* with other species in this genus.

We document here the distribution and aspects of ecology and biology of *Z. renardii*, and another species in the genus, *Zelus tetracanthus* Stål, which is also widespread in the Western USA and found in sympatry with *Z. renardii* in many areas. We documented the distribution ranges of both species based on records derived from museum specimens. Our field observations in Riverside County (Southern California) and in Baja California (Mexico) allowed us to investigate whether the 2 species are syntopic, i.e., encountered in the same habitat. Finally, we used laboratory cultures to study similarities and differences in predatory and reproductive behaviors in *Z. renardii* and *Z. tetracanthus*. These contributions will facilitate future, more detailed exploration of the relative invasive potential of species within *Zelus*.

Material and Methods

Distribution Maps

Specimens on loan from 11 natural history collections (see Acknowledgments) were examined and databased using the online PBI Plant Bug database (https://research.amnh.org/pbi/locality/). The databased samples comprised 1,613 specimens of *Z. tetracanthus* and 1,745 specimens of *Z. renardii*. Specimen data is publicly

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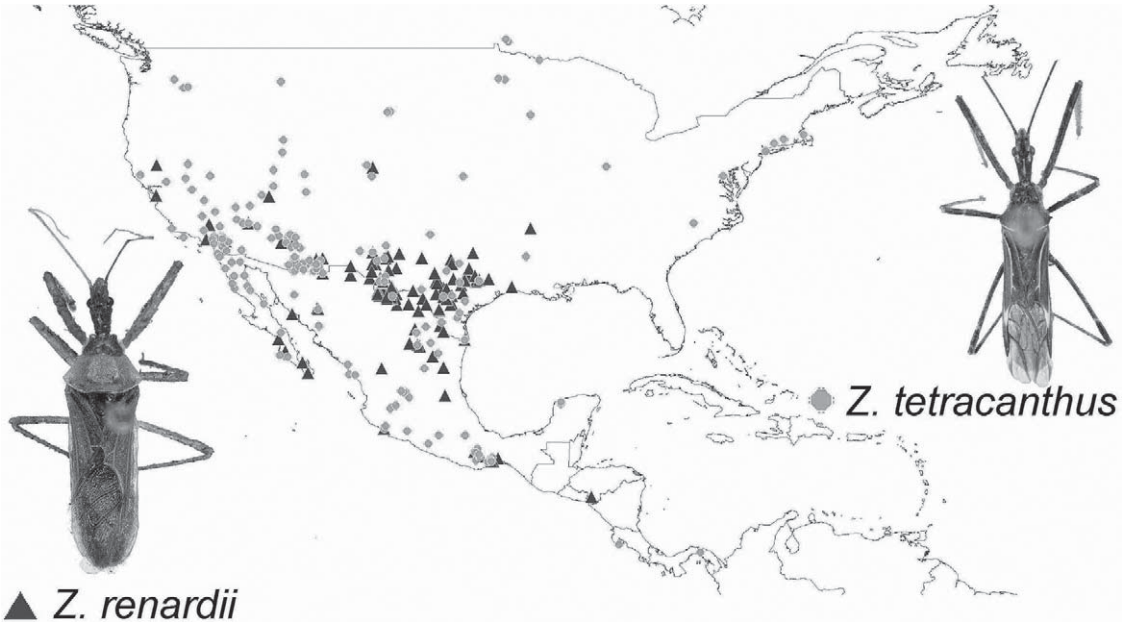


Fig. 1. Distribution of *Zelus renardii* and *Z. tetracanthus* in mainland North and Central America. The range of *Z. tetracanthus* extends to the east coast of North America, whereas *Z. renardii* is restricted to roughly the western half of the continent.

available through Discover Life (http://www.discoverlife.org/). Due to the geographic spread and number of records, these data provide the most comprehensive documentation of the distribution ranges of both species published to date. Many original locality labels lacked latitude and longitude information. These localities were georeferenced (i.e., latitude and longitude coordinates determined) using Google Earth, the USGS Geographic Names Information System (GNIS), or an online georeferencing gazetteer (http://www.fallingrain.com/world). The specimen data were mapped using the mapping feature of the AMNH PBI database (http://research.amnh.org/pbi/maps/). Distributions in North and Central America for both species are shown in Fig. 1. We used a map based on the Köppen climate classification to document climate zones for the plotted native range of *Z. renardii* and for the recorded extralimital distributions (Supplementary Fig. 1).

Documentation of Habitats for *Z. renardii* and *Z. tetracanthus* in Riverside County (California, USA) and Baja California (Mexico)

Collecting dates and elevations of collecting sites were summarized based on specimen records in the database. Habitats were described and photo-documented for several collection events of *Z. renardii* and *Z. tetracanthus* in Riverside County, California (2007-2010) and Baja California, Mexico (May 2008).

Behavioral Studies

Laboratory cultures were established from adult males and females collected in Riverside County (California) for *Z. renardii* and Madera Canyon (Pima County, Arizona; N 31.731 W 110.879) for *Z. tetracanthus*. Specimens were kept individually in petri dishes at constant room temperature (25 °C, 28% RH) and 12:12 h L:D (8 am-8 pm) under fluorescent lights and fed 10 adult *D. melanogaster* Meigen every 2 d. All petri dishes used in this study were Ø 90mm. To document predatory behaviors, an unfed assassin bug that had been starved for 3 d was placed under a Canon XL2 3CCD Mini DV video camcorder (Canon USA) in a petri dish, 10 adult *Drosophila melanogaster* were introduced simultaneously into the dish, and behaviors of the *Zelus* specimens were recorded on digital videocassettes (Mini DV; DVM60 ME). The cassettes were transferred to Windows Movie Maker (version 5.1; Microsoft) for analysis of behavioral sequences and to quantify the 1) time elapsed between introduction of the *Drosophila* into the petri dish and start of feeding (defined by the insertion of stylets into the prey item) and 2) feeding duration (time between insertion of stylets and dropping of prey item). Seven predation events for 7 different specimens were recorded for both species (Table 1).

To record mating behavior, one virgin male and one virgin female (aged 3-7 d after the final molt to assure sexual maturity) were placed together in a new petri dish and behaviors were recorded

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TABLE 1. DURATION OF PREDATORY BEHAVIORS (TO THE NEAREST MINUTE) FOR 2 SPECIES OF *ZELUS* (*N* = 14).

	Time to prey capture (min)			Duration of feeding (min)		
Species	Mean	SD	Range	Mean	SD	Range
Z. renardii	6.43 a	2.76	3-10	7.71 a	2.36	5-12
Z. tetracanthus	15.00 b	3.06	10-19	12.86 b	3.13	9-17

Letters within a column denote a significant difference between means ($P < 0.005$).

using the Canon XL2 system. Similar to the approach above, the video tapes were transferred to Windows Movie Maker for analysis of behavioral sequences and to quantify the 1) time elapsed between the introduction of pairs in the petri dish and start of copulation and 2) time elapsed from start (defined by aedeagus inserted) to end of copulation (male genitalia retracted). Twelve matings were recorded for *Z. renardii* and 15 for *Z. tetracanthus* (Table 2).

A Student's t-test (performed at http://vassarstats.net/) was used, assuming both equal and unequal variances, to determine if differences in feeding and mating times between the 2 species were significant. Statistical significance was always obtained whether assuming equal or unequal variances. We only report p-values assuming equal variances.

Each female was mated only once, the male removed after copulation, and the female was subsequently kept in a separate petri dish under the same environmental conditions as described above. The first deposited egg batch of each female was kept with the female and observed for emergence for 15 d or until immatures hatched (usually 8-12 d after deposition; see also Swadner & Yonke [1973]). We recorded the number of immatures that hatched from these egg batches.

RESULTS

Distribution Ranges of *Z. renardii* and *Z. tetracanthus* and Climatic Conditions in Areas of Introduction

Figure 1 shows what we consider to be the original distribution range of *Z. renardii* and *Z. tetracanthus* in North and Central America based on 3,358 specimen records. The 2 species are sympatric in, among other areas, the Western USA, including California and Baja California, Mexico, but also throughout part of Central America. The range of *Z. tetracanthus* extends to the east coast of North America, whereas *Z. renardii* is restricted to roughly the western half of the continent. In addition, *Z. tetracanthus* extends further north into Canada than *Z. renardii*. The ranges of both species extend over a number of different climatic zones, indicating that both species are capable of dealing with diverse abiotic environmental conditions. The simplified climatic world map combined with the known distribution of *Z. renardii* demonstrates that 3 of the areas where this species has been introduced are Mediterranean type climates (Chile, Greece, Spain), whereas Hawaii, Johnston Island and Samoa are wet tropical (Supplementary Fig. 1).

Habitats, Microhabitats, and Collecting Dates of *Z. renardii* and *Z. tetracanthus*.

The 2 species are sympatric over large parts of their ranges including the western USA and parts of Central America. *Zelus renardii* is found from slightly asl (above sea level; 8 m in Baja California, Mexico) to more than 2,000 m asl (Durango, Mexico). Adults have been collected every mo of the yr, but records between Nov and Feb are confined to Hawaii, Texas, and Mexico. Similarly, *Z. tetracanthus* has been recorded from localities at sea level (Baja California, Mexico) to 2500 m asl in the Chiricahua Mountains in Arizona. Collecting records indicate that the majority of North American specimens were collected between Apr and Oct and only 5 specimens in Dec (Arizona, California, Texas, and Baja California in Mexico).

The 2 species are syntopic at some localities. Supplementary Fig. 2 shows a habitat in Baja California where both species were very abundant on blooming *Prosopis* sp. (Fabales: Fabaceae) that at-

TABLE 2. DURATION OF MATING BEHAVIORS (TO THE NEAREST MINUTE) FOR *ZELUS RENARDII* (N = 12) AND *Z. TETRACANTHUS* (N = 15).

	Time to begin of copulation (min)			Duration of copulation (min)		
Species	Mean	SD	Range	Mean	SD	Range
Z. renardii	12.00 a	4.00	5-18	15.83 a	3.93	9-21
Z. tetracanthus	28.93 b	7.68	11-39	11.73 b	3.49	8-17

Letters within a column denote a significant difference between means ($P < 0.005$).

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tracted large numbers of insects, including plant bugs and bees. However, based on our collecting in Baja California and Riverside County, only 1 of the 2 species tended to be abundant in certain habitats. Supplementary Fig. 2B shows chaparral in the San Pedro Mártir mountains (Mexico, Baja California) at an elevation of ~1,100 m. *Zelus tetracanthus* was relatively common in this habitat on various species of shrubs and trees, but no *Z. renardii* were collected during the 2 collecting d one of the authors spent in this area. In contrast, numerous specimens of *Z. renardii* were collected by a team of 5 insect collectors sweeping vegetation, including blooming *Chilopsis* sp. (Bignoniaceae) in White Water Canyon in Riverside County, California (Supplementary Fig. 2C, D), but no *Z. tetracanthus* were netted. *Zelus renardii* is also very common in suburban yards in the Riverside city area (Supplementary Fig. 2E), but *Z. tetracanthus* is rarely found in developed areas. In suburban environments, *Z. renardii* is frequently found on native and non-native herbaceous and woody plants, including *Ceanothus* sp. (Rosales: Rhamnaceae), *Asclepias* spp. (Gentianales: Apocynaceae), and vegetables, such as tomato (*Solanum lycopersicum* L.; Solanales: Solanaceae) and pepper (*Capsicum* spp.; Solanales: Solanaceae). In addition to the adults, egg masses of *Z. renardii* were also frequently found attached to garden plants.

Observations on Predatory and Reproductive Behaviors of *Z. renardii* and *Z. tetracanthus*

Predatory Behavior

The components of predatory behavior were similar in *Z. renardii* and *Z. tetracanthus*. They consisted of antennal movement in direction of the prey (adult *D. melanogaster*); orientation and slow movement towards prey; raising of forelegs, labium, and antennae; striking; and insertion of stylets (Fig. 2A, B). This sequence was followed by an extended period of feeding, after which the fly was dropped and most assassin bugs engaged in cleaning behaviors. The 2 species differed dramatically not only in the amount of time that elapsed between the release of the fly into the petri dish and prey capture (t = 5.51, df = 12, P = 0.0001) but also in the actual feeding time (t = 3.47, df = 12, $P < 0.005$) (Table 1). *Zelus renardii* caught prey more quickly than *Z. tetracanthus* and also completed the entire feeding process in shorter time.

Reproductive Behavior

The behavioral components of mating were similar in the 2 species. The pre-copulatory behaviors comprised antennal movements of male and female from a distance and approach of the male. The male then assumed a dorsal riding position on the female (Fig. 2C, D), tapped the female's head and pronotum with the tip of his labium and embraced the female with his legs, followed by extension and rotation of the male genitalia (segment 8 and pygophore) and copulation (Fig. 2E, F). Mating attempts by males may fail at any of these steps as a result of the female's defensive behavior.

The time elapsed between the start of the trial (i.e., male and female assembled in petri dish) and copulation differed significantly (t = 6.91, df = 25, $P < 0.0001$) between the 2 species (Table 1). *Zelus renardii* individuals mated sooner on average than *Z. tetracanthus*. The average length of copulation differed significantly between both species (t = -2.98; df = 26, P = 0.006) (Table 2). *Zelus tetracanthus* pairs finished mating about 4 min sooner than pairs of *Z. renardii*.

The 2 species also differed in the ratio of egg batches from which first instars hatched, although the small sample size (only the first egg batch for each female was observed until hatching) did not allow for a statistical test of this result. In *Z. renardii*, immatures hatched from 8 of 12 egg batches (67%), whereas in *Z. tetracanthus* only 4 of 15 egg batches (27%) hatched.

Discussion

We compared native distribution ranges, habitat preferences, and certain biological features between the dispersalist *Z. renardii* and the closely related *Z. tetracanthus.* The observed similarities and differences stimulate additional hypotheses, some of which are outlined below, that upon testing may eventually explain why *Z. renardii* has become established outside its native range, but congeners have not. In the following, we discuss and evaluate our initial hypotheses on how original distribution range, habitat choices, and predatory and reproductive behavior might influence the dispersalist and invasive potential of *Z. renardii*.

Distribution Range

We proposed in the introduction that due to the large distribution range of *Z. renardii* across North and Central America, different populations may be pre-adapted to various climates, thus facilitating establishment under different climatic conditions; this ability may be absent in other *Zelus* species. We found that the distribution ranges of *Z. renardii* and *Z. tetracanthus* are broadly overlapping (Fig. 1); both species have native populations in tropical climates (large parts of Central America), dry, semi-arid and arid climates (Arizona and New Mexico in the USA), and Mediterranean climates (California, USA, and

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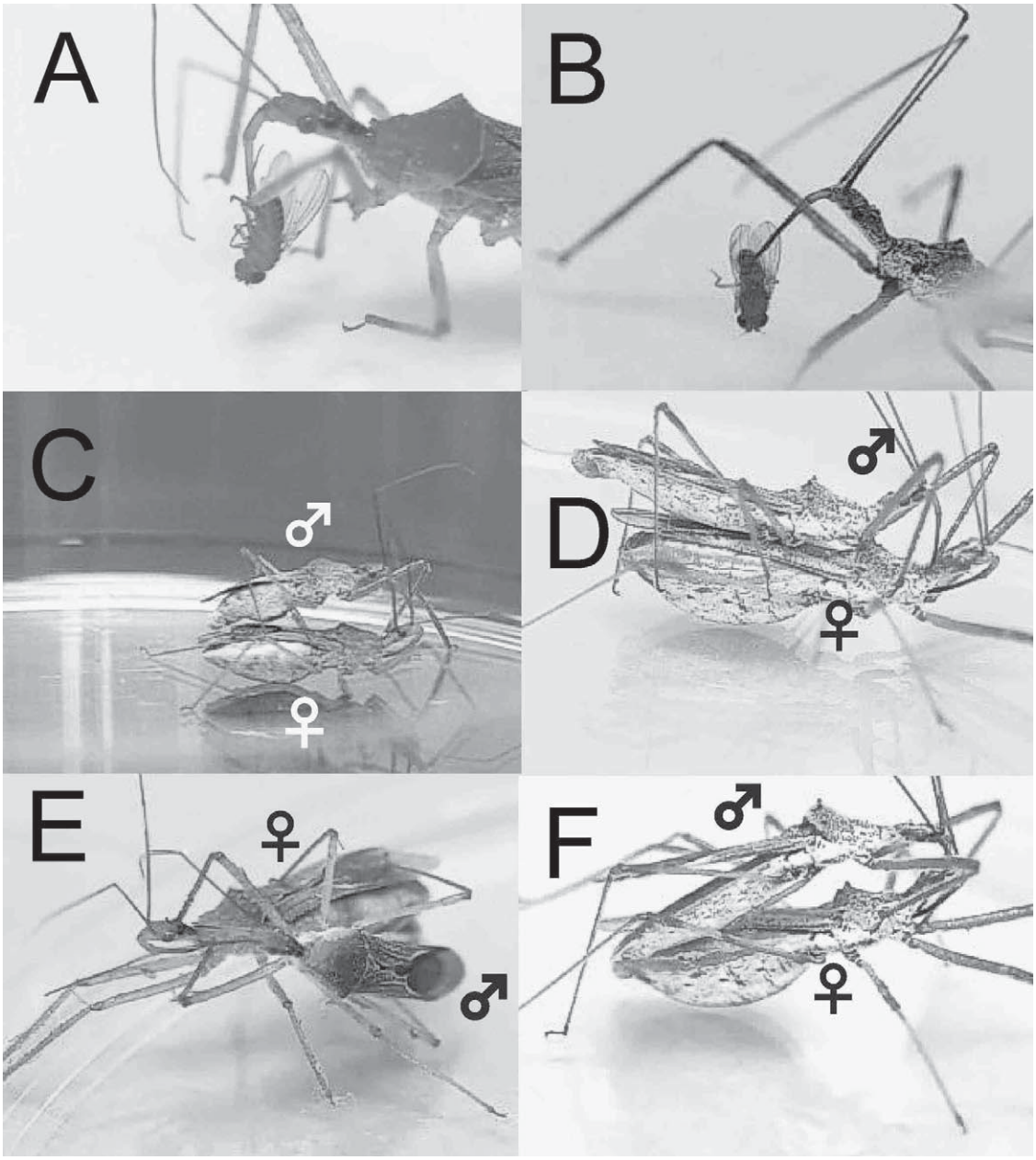


Fig. 2. Predatory and reproductive behaviors of *Zelus renardii* (A, C, E) and *Z. tetracanthus* (B, D, F). (A, B) Prey handling by *Zelus* spp. (C, D) pre-copulatory position in both species with the male assuming the dorsal riding position on top of the female. (E, F) Copulation in the 2 *Zelus* spp.

Baja California, Mexico). Based on these distribution ranges, populations of both species would be expected to have adapted to diverse climatic conditions.

The origins of the Hawaiian, Chilean, and European *Z. renardii* from populations in the native New World range are unknown; we also lack data that would indicate if the Greek and Spanish populations are independent invasions or based on a single introduction to Europe. We speculate that the populations that became established in tropical areas in the Pacific region may have originated from Central America, and the Chilean and European populations may be derived from Mediterranean climate adapted populations, e.g., in California. This hypothesis could be tested in the future using molecular markers and phylogeographic methods.

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Habitats and Microhabitats

Both species of *Zelus* are usually caught while beating and sweeping flowering and non-flowering vegetation. A pattern of host-plant preference is absent and both assassin bug species often seem to target flowering vegetation that attracts a diversity of potential prey items. Both species occupy various habitat types between the sea level and an altitude of up to 2,000-2,500 m. *Zelus tetracanthus* is more frequently confined to natural habitats that are relatively undisturbed by human activity. *Zelus renardii* occurs on a regular basis in agricultural settings and even urban and suburban environments, such as parks or other public spaces (i.e., our University campus). We have not surveyed plant nurseries, but would expect that *Z. renardii* is also common in such environments. *Zelus* females readily glue their egg batches on plants (usually on the ventral surface of the leaves) or other objects (i.e., tissue paper in the lab). These batches are typically firmly attached to the plant surface, eggs take 8-12 d to hatch, and immatures usually do not tend to disperse far from their egg batch during the first and second instars (C. Weirauch and G. Zhang, unpublished data.). We therefore propose that egg batches of *Z. renardii* may be shipped with nursery stock, presenting a possible avenue for their introduction to South America and Europe. Our observations indicate further that *Z. renardii* is more likely to be dispersed by humans than *Z. tetracanthus*, given the abundance of the former species in human-disturbed environments.

As indicated above, *Z. renardii* could be considered a pioneer species, and we suggest it might also be more tolerant to adverse conditions, such as high temperatures and scarce food supply, compared with its congeners. We do not have experimental data to support this argument, but our experience with collecting live specimens in the field and bringing them back to the lab to establish cultures provide some circumstantial evidence. Wild-caught *Z. renardii* specimens survive the transfer to the laboratory even under hot conditions, establish colonies easily, and even irregular food supply usually does not impact their reproductive success. This contrasts with *Z. tetracanthus*, which easily overheat and die during transport and appear to depend on more regular food supplies. The physiological properties of the 2 species warrant further study to evaluate how these factors may affect the survival rate of specimens during dispersal.

Predatory Behavior

Zelus renardii and *Z. tetracanthus* are of roughly the same total length (both of 12.5 mm, Hart 1986) and *Drosophila* flies appear to be suitably sized prey items for both species. *Zelus renardii* caught prey much faster upon release in the rearing container than *Z. tetracanthus*; *Z. renardii* also consumed drosophilid flies faster than its congener. Prey capture in the wild usually occurs on vegetation, and frequently, the assassin bugs remain rather exposed during capture and feeding (C. Weirauch, unpublished data). As a result, they may be more vulnerable to predation by predators such as birds. We hypothesize that under this scenario, the shorter predation and feeding time in *Z. renardii* might present an ecological advantage that reduces the risk of being preyed upon; and thus may contribute to the high abundance of this species in many areas.

Reproductive Behavior

The drastically different duration of pre-copulatory behaviors in the 2 *Zelus* species warrants further study. *Zelus renardii* engaged in copulation much more quickly than *Z. tetracanthus*. The male in the former species appeared rather "aggressive" in its approach to the female and copulation was achieved within 5 to 18 min, on average after 12 min, after the virgin pairs are assembled. Pre-copulatory behaviors in *Z. tetracanthus* ranged from 11 to 39 min and copulation began on average 29 min after introduction into the experimental chamber; the approach of the male is distinctly less aggressive than in *Z. renardii*. In this study, we did not evaluate details of the pre-copulatory behaviors beyond the general sequence of events that were similar in the 2 species (antennal movements of both sexes; approach of the male; male assumes dorsal position; tapping of female head and pronotum; genitalic extension). Given that prolonged pre-copulatory behaviors are often associated with chemical communication, additional studies should investigate a potential role of such compounds in the mating behavior of *Z. tetracanthus*. Edde & Phillips (2006) reported that males of *Z. tetracanthus* are attracted to bostrichid pheromone traps in the field. The bostrichid pheromone may act as a kairomone or aggregation pheromone, but it may also indicate that chemical communication could play a role in *Z. tetracanthus* mating behavior.

Another unexpected result was the dramatically different percentage of egg batches with viable first instars: 67% for *Z. renardii* and only 29% for *Z. tetracanthus*. These rates are based on egg batches derived from each of the females in this study, all of which were mated only once. We realize that our sample size is too small (n = 12 for *Z. renardii* and n = 15 for *Z. tetracanthus*) to draw far-reaching conclusions. We here propose 2 hypotheses as possible explanations for this greatly different number of first instars in the 2 species, which may deserve future examination. *Zelus tetracanthus* females, but to a lesser degree females of *Z. renardii*, may require mul-

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tiple matings to ensure fertile egg batches. This hypothesis can be tested with additional mating experiments. Secondly, and assuming that the lab conditions under which the 2 species were kept were not optimal, we propose that egg batches of *Z. renardii* may have higher tolerance to adverse environmental conditions (temperature, humidity), thus resulting in higher hatching rates. Such tolerance could be another important factor in allowing *Z. renardii* to be successful in pioneer situations and to quickly establish relatively high population densities.

In summary, *Z. renardii* and *Z. tetracanthus* show overlap in their distribution ranges and are exposed to the same range of climatic conditions throughout the Western United States; however, *Z. tetracanthus* occurs under a broader range of climatic zones than *Z. renardii*. The distribution range alone can therefore not explain the differential dispersal observed for the 2 species. *Zelus renardii* appears to be more abundant in man-made environments including gardens and parks; this association may facilitate dispersal by humans, i.e. with nursery stock. A comparative study of predatory behaviors indicated that *Z. renardii* spent less time preying, thus potentially evading vertebrate predators more readily than *Z. tetracanthus*. Comparisons of reproductive behaviors of the 2 species revealed that *Z. tetracanthus* was involved in more time-consuming pre-copulatory behaviors, indicating the potential role of chemical communications. *Zelus renardii* may be able to establish large populations faster than *Z. tetracanthus*, given the higher rate of viable egg batches produced. From our observations and experiments, we conclude that the association with humans that is observed in *Z. renardii* alone, but not *Z. tetracanthus*, may be the reason for the dispersal of this species; biological parameters including predation efficiency and higher rate of offspring per mating may further facilitate the establishment of this species outside its native range.

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