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Feign it till you make it: on the first comprehensive report of thanatosis in Cicadellidae (Hemiptera, Auchenorrhyncha) with morphological annotations and distribution of *Homalodisca ichthyocephala* (Signoret, 1854)

Fíngelo hasta que lo logres: sobre el primer informe completo de tanatosis en Cicadellidae (Hemiptera, Auchenorrhyncha) con anotaciones morfológicas y distribución de *Homalodisca ichthyocephala* (Signoret, 1854)

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ABSTRACT. The phytophagous insect family of leafhoppers (Hemiptera, Auchenorrhyncha, Cicadellidae) is widely distributed throughout the world's ecosystems, and Mexico houses a remarkable diversity of species and forms. The leafhopper genus *Homalodisca* (Hemiptera, Cicadellidae) includes key vectors of plant pathogens like *Xylella fastidiosa*. While some species are well-studied, the biology of others, such as *Homalodisca ichthyocephala*, remains largely unknown. This gap is particularly pronounced in ethology, as thanatosis (death-feigning) has never been formally documented for the diverse family Cicadellidae. Here, we present the first detailed analysis of this anti-predator behavior in *H. ichthyocephala* from Zirándaro, Guerrero, Mexico. Based on video analysis of 20 thanatotic events, five-sequence distinctive phases were identified: 1) Mechanical disturbance, 2) Catatonic, 3) Myoclonic, 4) Motor recovery, and 5) Escape. Overall females exhibited a significantly longer motor recovery than males (Mann-Whitney U test, W = 57.5, p = 0.03169). In addition to this behavioral analysis, an updated morphological diagnosis for *H. ichthyocephala*, clarifying several features insufficiently detailed in the original description, and presenting new records that significantly extend its known distribution within Mexico and Central America. In addition, habitat conditions with limited resources as found in the present study area are commented and other non-detailed cases of thanatosis known in the suborder are exemplified.

Key words: Leafhoppers, Guerrero, Zirandaro, Western Mexico, Cicadellinae, Proconiini

RESUMEN. La familia de insectos fitófagos conocida como chicharritas (Hemiptera, Auchenorrhyncha, Cicadellidae) se encuentra ampliamente distribuida en los ecosistemas del mundo, y México alberga una notable diversidad de especies y formas. El género de chicharritas *Homalodisca* (Hemiptera, Cicadellidae) incluye vectores clave de patógenos vegetales como *Xylella fastidiosa*. Aunque algunas especies han sido ampliamente estudiadas, la biología de otras, como *Homalodisca ichthyocephala*, sigue siendo en gran medida desconocida. Esta brecha es particularmente marcada en el ámbito de la etología, ya que la tanatosis (hacerse el muerto) nunca ha sido documentada formalmente para la diversa familia Cicadellidae. Aquí presentamos el primer análisis detallado de este comportamiento antipredador en *H. ichthyocephala* procedente de Zirándaro, Guerrero, México. A partir del análisis en video de 20 eventos de tanatosis, se identificaron cinco fases distintivas en secuencia: 1) perturbación mecánica, 2) catatónica, 3) mioclónica, 4) recuperación motora y 5) escape. En general, las hembras presentaron una fase de recuperación motora significativamente más prolongada que los machos (prueba U de Mann-Whitney, W = 57.5, p = 0.03169). Además del análisis conductual, se ofrece una diagnosis morfológica actualizada de *H. ichthyocephala*, aclarando varios rasgos descritos de forma insuficiente en la descripción original, y se presentan nuevos registros que amplían significativamente su distribución conocida en México y América Central. Asimismo, se comentan las condiciones del hábitat con recursos limitados presentes en el área de estudio y se ejemplifican otros casos de tanatosis poco detallados conocidos dentro del suborden.

Palabras clave: Chicharritas, Guerrero, Zirándaro, Occidente de México, Cicadellinae, Proconiini

INTRODUCTION

Leafhoppers (Hemiptera, Cicadellidae) are a highly diverse family within the order Hemiptera, comprising nearly 25,000 valid species worldwide (Dmitriev *et al.*, 2022-onward). All members of this group feed on plant vascular fluids (Dietrich, 2005). Those belonging to the subfamily Cicadellinae, are of either particular ecological or agricultural importance based on their apparently natural ability to transmit pathogenic mollicutes to a wide variety of economically significant crops around the globe (Bartlett *et al.*, 2018). Proconiini or commonly known as "sharpshooters", is one of the two tribes within the subfamily Cicadellinae and includes the major economic species of concern by transmitting *Xylella fastidiosa* Wells *et al.*, 1987 (Xanthomonadales: Xanthomonadaceae), where the sharpshooter genus *Homalodisca* Stål, 1869 with 17 valid species, are notable vectors for this xylem-dwelling bacterium across several crops such as grapevine, citrus, coffee, and almond (Cornara *et al.*, 2019).

Among species of *Homalodisca*, the glassy-winged sharpshooter (*H. vitripennis* (Germar, 1821)) is the most efficient and extensively studied vector. Meanwhile other species of minor importance, such as the smoketree sharpshooter (*H. liturata* Ball, 1900) and the Johnson grass sharpshooter (*H. insolita* (Walker, 1858)) are less surveyed. In contrast, *Homalodisca ichthyocephala* (Signoret, 1854) remains poorly documented and has been regarded only as a potential vector based on scattered records from Mexico and Central America (Murillo-Hernández *et al.*, 2020). During a recent field study conducted in Guerrero of this little-known species, we documented a previously unreported thanatotic behavior for the family Cicadellidae.

Thanatosis or tonic immobility (TI), commonly referred to as death-feigning or playing possum, is a well-known, anti-predator behavioral mechanism characterized by a state of motionlessness in response to external stimuli observed across a wide range of animal taxa (Humphreys & Ruxton, 2018). TI is present in both vertebrates and invertebrates (Cassill *et al.*, 2008); however, its scattered and often anecdotal occurrence suggests that it has evolved independently across diverse lineages. This is mainly explained by the simplicity of the behavior and its role as a last-resort defense when fleeing or fighting is not possible. Altogether, this supports the idea of convergent evolution driven by similar ecological pressures (Humphreys & Ruxton, 2018). However, most cases of insects are poorly understood because of fortuitous findings and lacking details.

TI represents a widespread but taxonomically uneven anti-predator strategy across insects, largely notable examples occurring in Phasmida and Hymenoptera (Humphreys & Ruxton, 2018). The Indian Stick Insect *Carausius morosu*s Brunner von Wattenwyl, 1907 (Phasmida, Lonchodidae) exemplifies how TI exploits predator cognition, inexperienced birds that learned dead stick insects were unpalatable and subsequently avoided live insects displaying thanatosis (Skelhorn, 2018). Among social insects, the fire ant *Solenopsis invicta* Buren, 1972 (Hymenoptera, Formicidae) shows age specific TI deployment, with young workers feigning death during intraspecific conflicts to survive attacks from older nestmates (Cassill *et al.*, 2008). These cases highlight TI's dual roles in interspecific predator avoidance and intraspecific conflict resolution, though its scattered distribution across insect orders such as Coleoptera, Plecoptera, Lepidoptera, Odonata, and among others suggest complex evolutionary pathways (Humphreys & Ruxton, 2018).

Within Hemiptera, known reports of TI remain exceptionally rare, with most cases occurring in the suborder Heteroptera. The harlequin cabbage bug *Murgantia histrionica* (Hahn, 1834) (Hemiptera, Pentatomidae) exhibits ontogenetic shifts on TI expression with its first instars feigning death more often than the chemically defended older nymphs and adults (Guerra-Grenier *et al.*, 2021). On another hand, *Oplomus catena* (Drury, 1782) (Hemiptera, Pentatomidae) displays this behavior only in adults with both the legs and the antennae extended, suggesting a species-specific ontogenic pattern in the expression of TI at least in the family Pentatomidae (Brugnera *et al*., 2019). Another example is the coreid bug *Merocoris distinctus* Dallas, 1852 (Hemiptera, Coreidae) which displays an elaborate TI sequence involving ventral exposure ending with an acrobatic recovery jump (Peraza-Sánchez, 2024). TI in Heteroptera is not limited to terrestrial insects, when disturbed, some water scorpions from the family Nepidae such as *Nepa cinerea* Linnaeus, 1758 (Hemiptera, Nepidae) assume a rigid posture with its legs pressed against the abdomen and raptorial forelimbs extended forward, and *Ranatra linearis* (Linnaeus, 1758) (Hemiptera, Nepidae) which remains motionless for up to an hour, mimicking inanimate debris (Hanel, 2021).

Inside Auchenorrhyncha, TI remains relatively understudied and is rarely emphasized in taxonomic literature. The most notable and well-documented examples are *Nyara thanatotica* Villet, 1999 (Hemiptera, Cicadidae) or "Drab Fainting Cicada," which drops motionless when disturbed (Villet, 1999), and the spotted lanternfly *Lycorma delicatula* (White, 1845) (Hemiptera, Fulgoridae) which displays a sequential antipredator strategy involving escape, deimatic display and TI with a clear seasonal pattern in which early-season adults tend to flee, while late-season individuals predominantly feign death (Kang *et al*., 2016).

In contrast, TI has not been formally documented in Cicadellidae, although some isolated reports describe behaviors resembling death-feigning. Chiykowski (1977) briefly noted that adults of *Aphrodes bicincta* (Schrank, 1776) (Hemiptera, Cicadellidae) drop to the ground and feign death when mechanically disturbed. Similarly, Hamilton and Zack (1999) mentioned that disturbed females of the genus *Errhomus* Oman, 1938 (Hemiptera, Cicadellidae) retract their legs and fall from the plant. In both cases, the authors only briefly referred to this death-feigning behavior without explicitly identifying it as TI or providing further details about the behavioral pattern. It is quite remarkable that one of the authors also found anecdotal evidence suggesting that *Osbornellus* Ball, 1932 (Hemiptera, Cicadellidae) may exhibit similar behavior (Suppl. 1), although none have explored it in greater detail.

Conversely in this context, the rarity of TI records known into Auchenorrhyncha, combined with the present discovery of thanatosis in *Homalodisca ichthyocephala* (Signoret, 1854) (Hemiptera, Cicadellidae) makes this case exceptionally relevant as the first detailed report for the speciose leafhopper family. This study was conducted in Zirándaro, State of Guerrero, Mexico, a region largely characterized by dense coverage of seasonally tropical dry forests. The overall observations were recorded in a semi-rural garden continuously irrigated year-round. The environment played a crucial microhabitat contrasting to the surrounding vegetation and land, which is dominated by arid cattle-grazing pastures and monoculture maize fields. In this contribution, we aimed to document extensively the overall behavioral thanatosis pattern based on direct *in situ* observation of adult males and females of *H. ichthyocephala* in the Balsas Basin biogeographic province. In addition to reporting this new behavioral trait in leafhoppers, a detailed diagnosis for this species and updated distributional data are provided.

MATERIALS AND METHODS

Fieldwork was conducted in Zirándaro de los Chávez, municipality of Zirándaro, State of Guerrero, Mexico (18°28'8''N, 100°58'55''W). Behavioral specimen observations *in situ* were documented from April 13th to 19th and from July 23th to 26th, 2025. Male and female adult specimens of *H. ichthyocephala* were taken using a prototype of portable light trap (Pinedo-Escatel *et al*.

unpublished) within an isolated semi-rural garden area. Location is monthly irrigated, and vegetation is composed of the next ornamental and orchard plants: "Reunión de señoritas" (Gentianales, Rubiaceae, *Ixora* spp. L.), mango (Sapindales, Anacardiaceae, *Mangifera indica* L., 1753, non Blume, 1827 nec Wall.,1847), almond (Rosales, Rosaceae, *Prunus dulcis* (Mill.) D. A. Webb, 1967), tamarind (Fabales, Fabaceae, *Tamarindus indica* L.), mandarin (Sapindales, Rutaceae, *Citrus* × *tangerina* Tanaka), Mexican lemon (Sapindales, Rutaceae, *Citrus* × *aurantifolia* (Christm.) Swingle), bougainvillea (Caryophyllales, Nyctaginaceae, *Bougainvillea* spp. Comm. ex Juss., 1789), jasmine (Lamiales, Oleaceae, *Jasminum* spp. L.), "Palma orejona" (Alismatales, Araceae), and "cuachalalate" (Sapindales, Anacardiaceae, *Amphipterygium adstringens* (Schltdl.) Schiede ex Standl.), among others. Microhabitat is humid in contrast to the predominant Seasonally Dry Deciduous Forest with extensive agricultural and grazing areas characterizing the region. Vegetation surrounding the collecting site is mainly composed of characteristic seasonally tropical plants such as: *Vachellia* spp., *Acrocomia aculeata* (Jacq.) Lodd. ex Mart, *Neobuxbaumia* spp., *Conzattia multiflora* (B.L.Rob.) Standl, and *Bursera* spp.

Specimens of *H. ichthyocephala* resting on the light trap were picked up by hand and placed in the palm to repeatedly observe the thanatotic behavioral pattern following next systematic procedure and taking into consideration Rogers and Simpson's (2014) concept, which consists in five distinct phases (Fig. 1 and Suppl. 2) comprising overall phenomenon: (1) MD: Mechanical disturbance, (2) CA: Catatonic, (3) MY: Myoclonic, (4) MR: Motor recovery, and (5) ES: Escape. The entire sequence of each phase was video recorded using a mobile device then processed individually and gathered data analyzed as a whole.

After recording all individuals events on each thanatosis phase, specimens were placed in 96% ethanol and brought to the Colección Nacional de Insectos (CNIN) of the Instituto de Biología, Universidad Nacional Autónoma de México (IB-UNAM) to complete processing by pinning and examine male abdomens to identify specimens under morphological comparison following the leafhopper´s protocol of Pinedo-Escatel *et al*. (2025) and Acevedo-Reyes *et al*. (2019), with the next modifications: cleared in hot 15% KOH (provided by Laboratorio Nacional de Microscopía y Fotografía de la Biodiversidad - LANABIO), rinsed and shaken twice for five minutes each in test tubes with distilled water, soaked in clove oil for one minute to stabilize remaining KOH, a second round of rinsed and shaken but with 96% ethanol during five minutes, and then attached beneath specimen in microvials with glycerin.

Overall habitus photographs were taken at the LANABIO of the IB-UNAM using a Carl Zeiss™ AXIO Zoom.V16 stereomicroscope equipped with a Zeiss™ Axiocam MRc5 camera and ZEN™ (Zeiss Efficient Navigation) Pro-2012 software. All digital photographs were taken from a Plan-NEOFLUAR Z 1.0x/0.25 FWD 56 mm objective. Measurements were extracted from an electronic vernier and corroborated with ImageJ software (imagej.nih.gov). All material studied is deposited at the CNIN of the IB-UNAM.

Statistical analyses and table generation were performed using R version 4.5.0 under "How About a Twenty-Six" (2025-04-11). Descriptive statistics (minimum, maximum, and mean) were calculated for the duration of each behavioral phase. Furthermore, the non-parametric Mann-Whitney U test was used to evaluate sex differences considering the duration of the CA, MY and MR. Image editing was carried out with GIMP 3.0.4 (GNU Image Manipulation Program) and Adobe Photoshop version 21.2.2. Illustrative diagrams were created using Clip Studio Paint EX (64-bit) version 3.1.0.

RESULTS

Thanatotic behavioral pattern. Five distinct phases of TI were identified in *Homalodisca ichthyocephala*: the MD referring to the initial external stimulus that mimics a predatory attack or entrapment; in this study, it was induced manually by disturbing each individual and placing it dorsum-down. This triggered the subsequent CA, characterized by a rigid, motionless posture that represents the core of the thanatotic response, feigning death to deter predation. The following MY marked by abrupt, uncoordinated muscular activity aimed at restoring a natural stance. Then, the MR involves the gradual regain of postural control and coordinated movements. Finally, the ES occurs when the individual actively flees out from the perceived threat (Figs. 1 and 2).

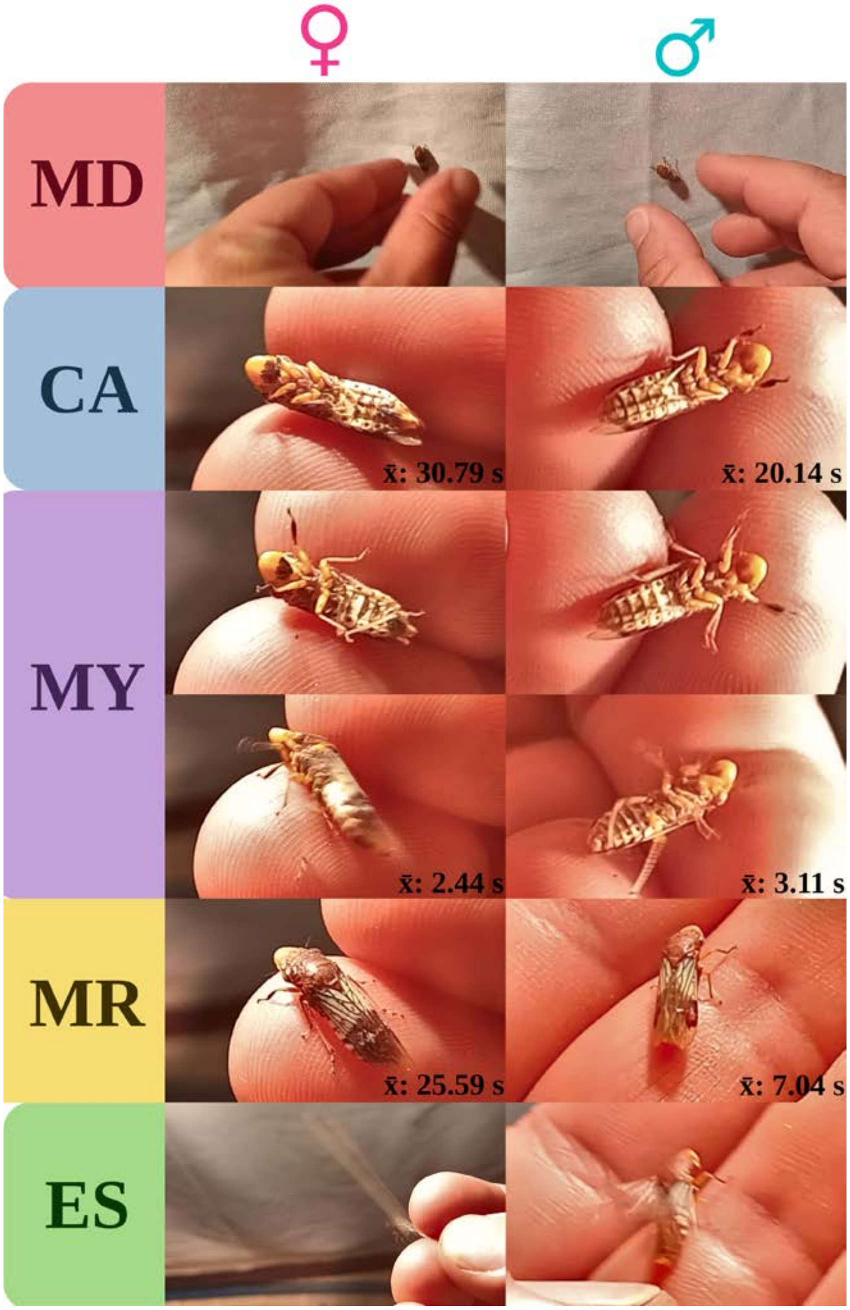

Figure 1. Frames of *in situ* observation and record of overall thanatotic behavior of *Homalodisca ichthyocephala* (Signoret, 1854) (Hemiptera, Cicadellidae).

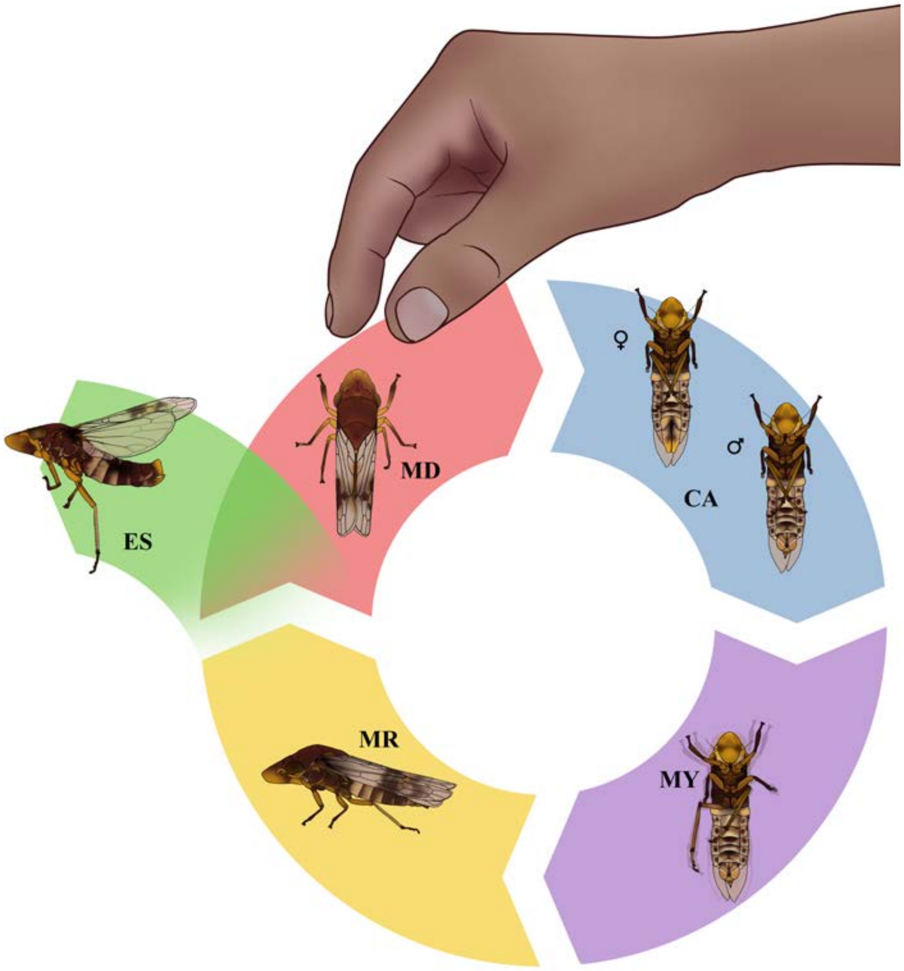

Figure 2. Illustrative schematic pattern of five thanatotic phases of *Homalodisca ichthyocephala* (Signoret, 1854) (Hemiptera, Cicadellidae). MD = Mechanic disturbance, CA = Catatonic, MY = Myoclonic, MR = Motor recovery, ES = Escape.

A total of 20 thanatotic events were video recorded and analyzed for *H. ichthyocephala*. Of these, 60% (n=12) were associated with females, while males accounted for eight events (40%) (Table 1 and Fig. 3). All individuals entered a rigid and motionless state immediately upon capture, corresponding to the CA. During this phase, both males and females consistently extended their forelegs while folding their mid and hind legs against the thorax. The CA showed considerable variation in duration, ranging from 1.17 seconds to 1 minute 51.06 seconds. Females exhibited a mean CA duration of 30.8 seconds (±29.8 s), while males showed a mean of 20.1 seconds (±13.0 s), indicating a trend toward longer catatonic responses in females (Figs. 1 and 2).

The MY was observed in 13 out of the 20 recorded events (7 females and 6 males). MY durations ranged from 0.07 to 12.2 seconds, with most cases lasting under 5 seconds. The MR was consistently observed in all individuals except for two females and one male, which did not resume a normal posture during the observation window and flew away immediately. MR durations varied broadly, from an instantaneous recovery to 1 minute 23.20 seconds. In general, females displayed longer MR (mean = 25.6 s) compared to males (mean = 7.04 s), although the high variability among individuals suggests the influence of additional, uncontrolled factors. One individual of each sex unexpectedly displayed more than one thanatotic episode during the observation period, suggesting that the behavior could be repeated under consecutive disturbances (Figs. 1 and 2).

Overall, females tended to display longer, and more variable CA durations (mean = 30.8 ± 29.8 s) compared to males (20.1 ± 13.0 s), as well as slower and more variable MR (25.6 ± 25.1 s vs. 7.04 ± 3.31 s). Males, on the other hand, exhibited the MY more frequently (75% of cases vs. 58.3% in females), with greater variability in duration (up to 12.2 s) (Table 1, Fig. 3).

Table 1. Thanatotic behavior phases in *Homalodisca ichthyocephala* (Signoret, 1854) (Hemiptera, Cicadellidae): Duration of catatonic (CA), myoclonic (MY), and motor recovery (MR) phases by individual. Measurement units = seconds (s).

Individual ID	**CA (s)**	**MY (s)**	**MR (s)**
Female1_16iv25	42.04	4.01	19.25
Female2_16iv25	8.17	1.15	0.00
Female2_16iv25_2	17.23	0.27	14.26
Female3_16iv25	38.04	0.13	52.24
Female4_16iv25	33.23	0.00	37.00
Female5_16iv25	1.17	2.08	16.08
Female1_17iv25	24.16	5.28	7.25
Female2_17iv25	8.15	0.00	0.00
Female3_17iv25	111.06	0.00	83.20
Female1_18iv25	27.02	4.18	15.26
Female1_19iv25	52.23	0.00	6.24
Female2_19iv25	7.02	0.00	5.08
Male1_16iv25	45.21	0.00	0.00
Male2_16iv25	25.06	4.03	12.27
Male3_16iv25	27.01	0.17	6.02
Male1_17iv25	4.12	0.11	9.06
Male1_17iv25_2	15.29	0.07	8.26
Male1_19iv25	6.17	12.18	4.29
Male2_19iv25	18.15	2.13	2.11
Male3_19iv25	20.12	0.00	7.25

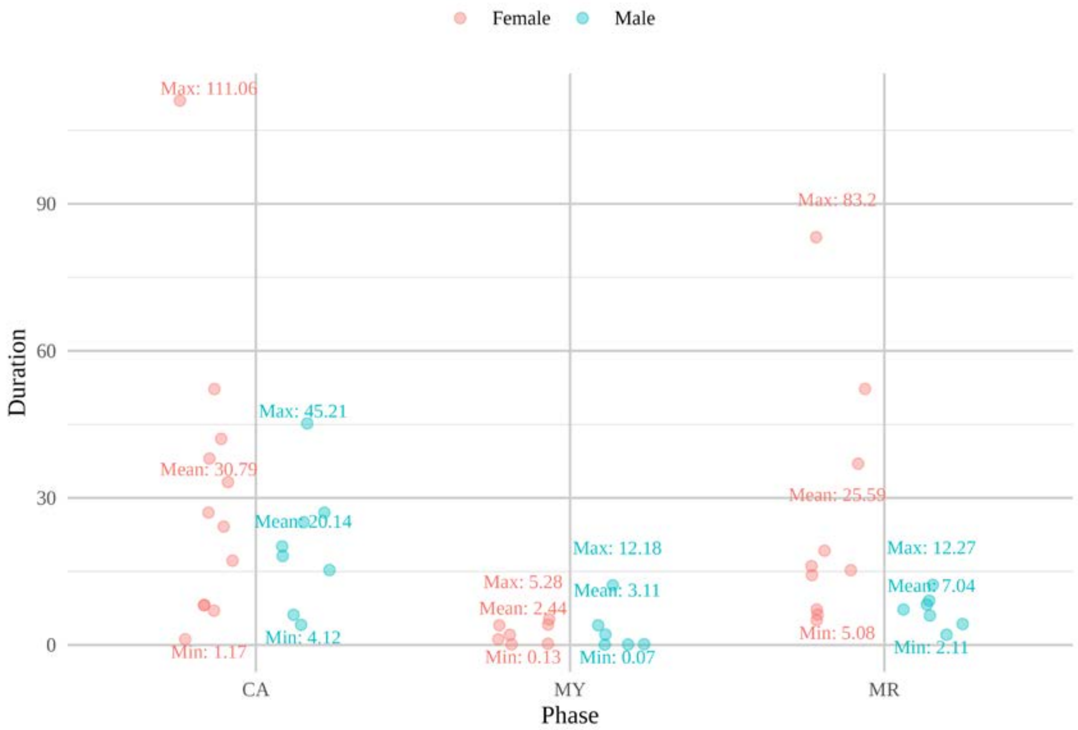

Figure 3. Range of thanatosis duration per phase between males and females of *Homalodisca ichthyocephala* (Signoret, 1854) (Hemiptera, Cicadellidae).

Statistical analyses using the Mann–Whitney U test indicated no significant sex differences in the duration of the CA (W = 58, p = 0.4636) and MY (W = 25, p = 0.6171) phases. However, females exhibited significantly longer MR durations compared to males (W = 57.5, p = 0.03169).

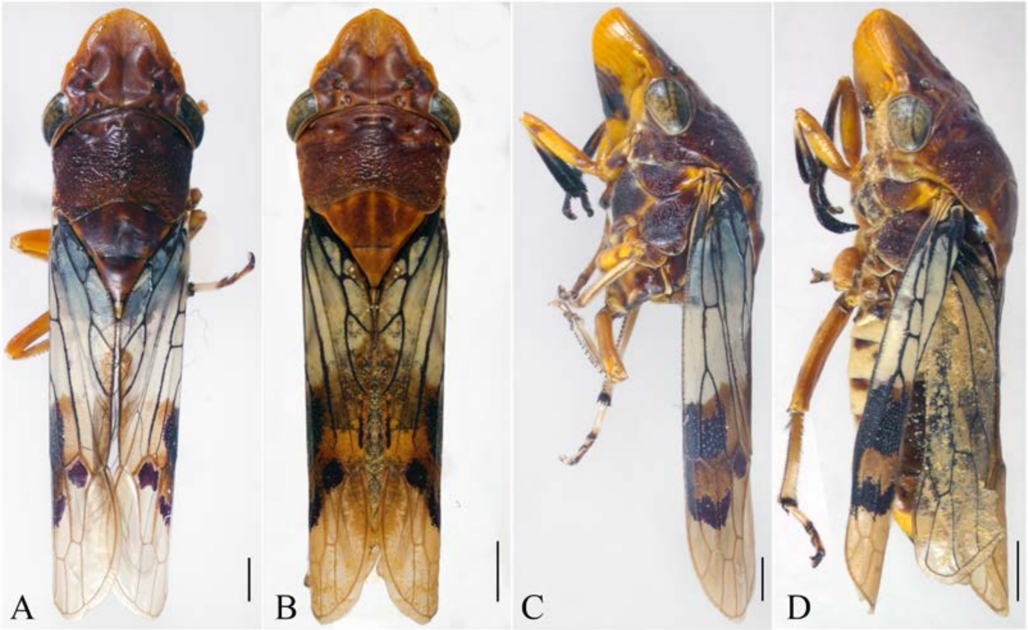

Figure 4. Dorsal and lateral habitus of male (A and C) and female (B and D) of *Homalodisca ichthyocephala* (Signoret, 1854) (Hemiptera, Cicadellidae).

***Homalodisca ichthyocephala* (Signoret, 1854)**

Tettigonia ichthyocephala Signoret, 1854: 494 (original description).
Proconia ichthyocephala (Signoret, 1854) in Walker (1858: 229).
Tettigonia ichthyocephala Signoret, 1854 (subjective synonym of *Tettigonia vitripennis* Germar, 1821) in Fowler (1899: 221).

Homalodisca ichthyocephala (Signoret, 1854) in Young (1968: 196). Figures 4-6.

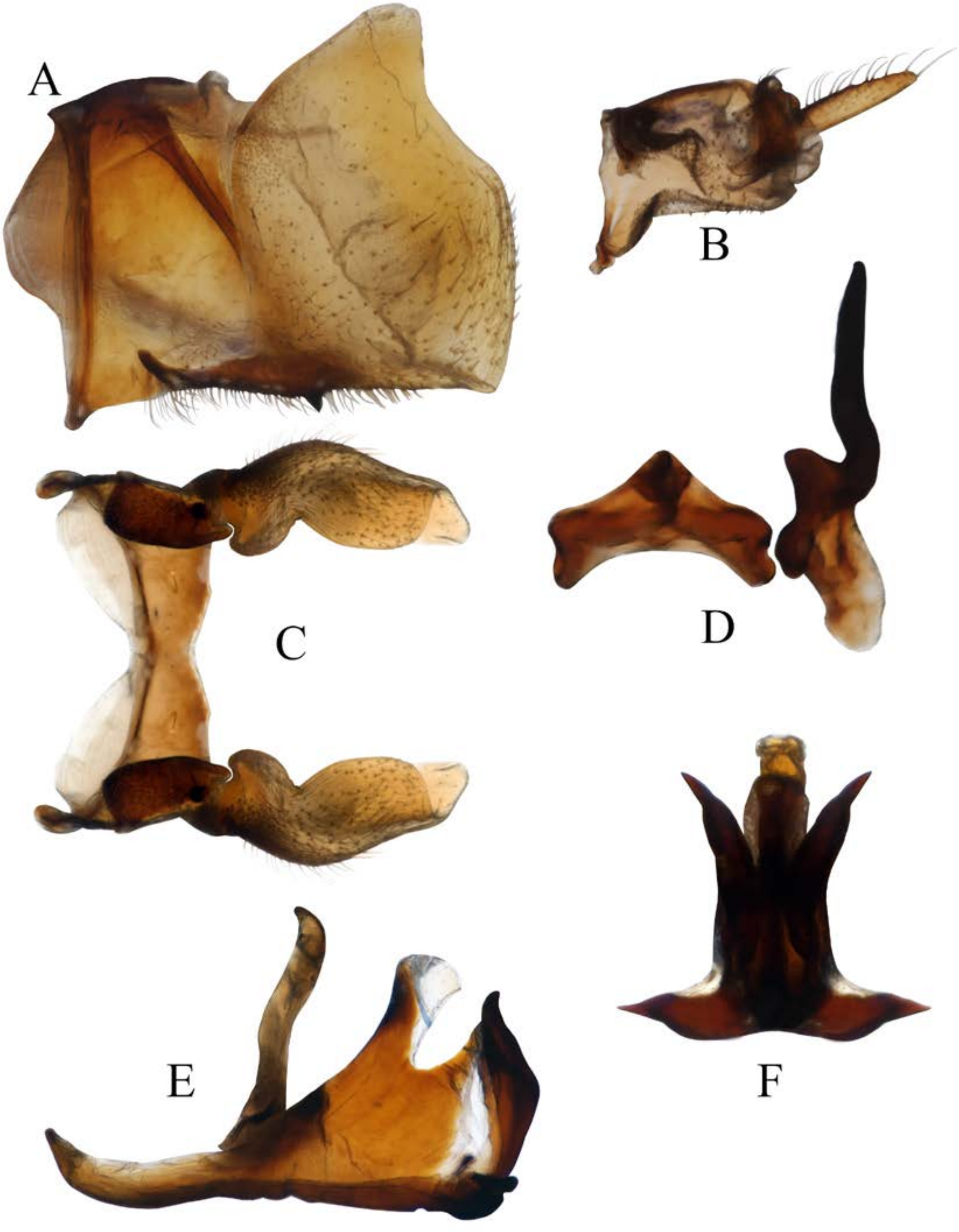

Figure 5. Male genitalia of *Homalodisca ichthyocephala* (Signoret, 1854) (Hemiptera, Cicadellidae). A = Pygofer, lateral view. B = Anal tube, lateral view. C = Pygofer, ventral view. D = Style and connective, ventral view. E = Aedeagus, lateral view. F = Aedeagus, posterior view.

Figure 6. Female VII sternite of *Homalodisca ichthyocephala* (Signoret, 1854) (Hemiptera, Cicadellidae), ventral view.

Morphological remarks. Body robust, length 10.5–11 mm in males and 11–12.5 mm in females. Overall color fades from light brownish to reddish with black, yellowish, and pale marks on dorsum and venter (Fig. 4 A–D). The crown is 1.5 times wider than long; sutures blackish; surface irregular and mostly with smooth texture. Ocelli black or green; not equidistant to eye and midline; rounded. Eyes in anterior view swollen; prominent; and green. Frontoclypeus totally yellowish, or if partially, the upper zone is yellowish and bottom mostly blackish; without fine setae. Anteclypeus black with yellow lateral margins. Pronotum 1.8 times wider than long; anterior margin almost straight with slight medial projection, but not beyond the eyes; posterior margin strongly notched; surface anteriorly smooth with four deep dots and posterior punctate; lateral carina well carinate and as long as width of eye. Scutellum with an anterior margin wide, as posterior margin of pronotum width, reddish to orange in color. Forewing with no false cells, anteriorly pale and distally black with red spots. Legs yellowish and sections of the femur and tibia blackish. Abdomen yellow, with pale and black irregular marks on dorsum, lateral, and venter. Pygofer subrectangular; anterior margin displaying long apodemes; 2.1 times longer than tall; dorsal margin well sclerotized but posterior weaker, and ventral strongly sclerotized with stout tooth on mid length; posterior margin preapically excavated and ventral sinuous (Fig. 5 A and B). Anal tube cylindrical, membranous, and 1.2 times longer than wide (Fig. 5 B). Valve narrow, 3.5 times wider than long. Subgenital plate triangular; uniseriate with 13 to 17 macrosetae; outer and inner margins straight. Connective short. Style basally rounded; mid lobe strongly projected; apophysis long with apex digitate; surface smooth; without fine setae or teeth (Fig. 5 D). Aedeagus prominent contrasting male capsule size; in lateral view strongly projected (Fig. 5 E); in poster view with four two pairs of acute processes, one up directed posterad and another down pointing laterally (Fig. 5 F). Female much as male but darker in overall color; VII sternite deeply excavated medially (Fig. 6).

Specimens examined. 25♂, 29♀ (CNIN) – Mexico: Guerrero, Zirándaro, Zirándaro de los Chávez, 18°28'8''N 100°58'55''W, 216 m, 15-Abril-2025, Vega-Ovando F.R. Col., Trampa Luz [MEXGUE401].

Distribution. Mexico, Guatemala, Honduras, Nicaragua, El Salvador, and Costa Rica (Fig. 7).

State records in Mexico. Baja California, Chiapas, Colima, Guanajuato, Guerrero, Jalisco, Michoacán, Morelos, Nayarit, Nuevo León, Oaxaca, Quintana Roo, Sinaloa, Sonora, Tamaulipas, and Yucatán (Fig. 7).

Figure 7. Map of distribution of *Homalodisca ichthyocephala* (Signoret, 1854) (Hemiptera, Cicadellidae) in Mexico and Central America.

Host plants. *Citrus* spp. (Rutaceae) and *Mangifera indica* (Anacardiaceae).

Notes. Young (1968) noted that morphology of *H. ichthyocephala* could slightly vary based on the locations where specimens were taken. Here using a larger specimen-sample (see material examined) we add morphological details not considered in previous sources regarding particular information of this species to make clearer its segregation from other congeneric relatives.

DISCUSION

While collecting specimens attracted to the light trap, one individual of *Homalodisca ichthyocephala* was taken for sex determination. Unexpectedly, the specimen became motionless between our fingers. At first, this reaction was attributed to excessive handling pressure that might have injured or killed the insect. However, the recurrence of the same pattern across several individuals soon revealed a consistent and repeatable behavioral response. This serendipitous observation led us to systematically document and describe for the first time the thanatotic behavior in *H. ichthyocephala*.

Remarkably, the observations conducted during the dry season provided valuable insights despite the generally lower insect activity expected, even within restricted humid environments (Lara-Pérez *et al*., 2023). Although the sampling area was small, mirroring the limited sample size obtained, the use of a light trap facilitated specimen attraction even during the region's most severe drought period on record (Mendoza-Uribe & Vázquez-Zavaleta, 2017). Despite these restrictive conditions and the reduced number of individuals, every specimen collected exhibited the thanatotic response.

Given the total (n= 20) number of behavioral observations video recorded and selecting two categorical groups (sexes), the non-parametric Mann–Whitney U brought informative data for most phases (>p= 0.05). Overall results show that females tended to display longer and more variable CA and MR, whereas males more frequently exhibited the MY. The Mann–Whitney U test revealed a significant difference only in MR duration (longer in females), yet this isolated result is insufficient to confirm a consistent sex-based pattern in TI expression. Instead, the high variability observed across individuals and phases suggests that TI in *H. ichthyocephala* is shaped by a combination of intrinsic and contextual factors, rather than by sex alone.

The study site, a small garden surrounded by a dense seasonally tropical dry forest functioning as a microhabitat of amid pastures and reckless lots during the dry season, likely imposed additional ecological constraints with greater opportunities for certain taxa (e.g., *Renonus* in Pinedo-Escatel, 2025; Lara-Pérez *et al*., 2023). The scarce availability of resources and shelter in the surrounding area may have influenced individual energy reserves, potentially leading to longer or more variable recovery times in some individuals, as energy depletion under resource limitation has been shown to affect metabolic recovery and activity levels in insects (Zhang *et al*., 2019). However, further research conducted across different seasons and habitat conditions will be necessary to determine whether such environmental stressors play a consistent role in shaping the expression of thanatosis.

Cases of TI are notoriously difficult to detect in the field (Humphreys & Ruxton, 2018), especially among small and elusive insects such as leafhoppers, where escape responses usually dominate. Also, documenting TI in *Homalodisca* therefore contributes valuable evidence to understanding the ecological contexts of anti-predator strategies in Auchenorrhyncha.

To contextualize our findings within a theoretical framework, we turned to the model proposed by Rogers and Simpson (2014), and according to this replica, we identified two thanatotic phases, induction and maintenance, explaining a neuromuscular mechanism involved. Following the stated framework, our behavioral observations in *H. ichthyocephala* allowed us to refine this process into five distinct externally observable phases. The MD and CA can be conceptually grouped under the induction stage, while the MY corresponds to the maintenance stage as earlier defined in crickets (Rogers & Simpson, 2014). MR and ES may represent a post-maintenance recovery process. Although our categorization is based on direct response, all behavioral observations made on *H. ichthyocephala* were consecutively repeated indistinctly between males and females.

Current documentation of thanatosis in *H. ichthyocephala* stands out for the following reasons: first, it represents the underlying detailed report of TI in the vast family Cicadellidae

(Dmitriev *et al*., 2022–onward), without formal mention of this behavior in the literature. Previously known scattered notes (e.g., for *Aphrodes bicincta* in Chiykowski (1977) and *Osbornellus* in Suppl. 1) lacked standardized behavioral descriptions or phase-based characterization. Second, the five-phased model captures the sequence and dynamics of TI in this xylem-feeding sharpshooter, which might also offer a framework for comparative studies across Cicadellidae and related taxa.

When placed alongside other documented cases of thanatosis in Auchenorrhyncha, both parallels and distinctions emerge. For instance, the cicada *Nyara thanatotica* Villet, 1999 exhibits a similar death-feigning response (Villet, 1999), but no subdivision of the behavior into phases or analysis of intersexual variation has been attempted. In the spotted lanternfly, *Lycorma delicatula*, TI is embedded in a broader antipredator strategy that includes dramatic display and escape behaviors (Kang *et al*., 2016), suggesting that behavioral complexity may increase with ecological and developmental pressures. In contrast, *H. ichthyocephala* responds consistently with a rapid, multi-phase immobility under minimal mechanical disturbance, indicating a potentially innate and stereotyped antipredator mechanism.

Beyond Auchenorrhyncha, many heteropteran examples showed that TI is often modulated by developmental stage, morphology, or ecological niche. As reported in *Murgantia histrionica* (Guerra-Grenier *et al*., 2021), *Oplomus catena* (Brugnera *et al*., 2019), and *Merocoris distinctus* (Peraza-Sánchez, 2024) exhibiting variation in posture and duration, sometimes involving complex recovery behaviors or sex-based differences. Remarkably, *H. ichthyocephala* also displays stereotyped leg positioning during the CA phase and subtle sexual dimorphism in recovery time, reinforcing the notion that TI is not a mere reflex, but a behavior modulated by internal and external cues. Nevertheless, and opposite to beforementioned, aquatic Heteroptera, such as *Ranatra linearis* and *Nepa cinerea*, present another dimension of TI expression: long-lasting, static responses likely shaped by predator dynamics in these habitats (Hanel, 2021). The shorter and more abrupt response of *H. ichthyocephala* may reflect selection for quick recovery in sun-exposed, predator rich environments, where delayed escape could be lethal.

Isolated areas as our study site, according to Janzen (2004), could act as a humid refuge within an otherwise xeric landscape, ultimately providing a rare opportunity to observe behavioral responses under natural yet constrained ecological conditions (Lewis & Basset, 2007; Janzen, 2004). These findings highlight the potential plasticity and context-dependence of this behavior and emphasize the importance of *in situ* behavioral studies in leafhoppers, a group for which ethological data remains critically scarce, and a field within entomology poorly investigated. In addition to describing the behavioral sequence of TI, this study also provides an updated morphological diagnosis and extends the known distribution of *H. ichthyocephala* in Mexico. These additions are relevant because several morphological features were not clearly detailed in the original description by Signoret (1854) or the redescriptions by Young (1968). Furthermore, the new distributional records exemplify and refine the geographic range of this species, which had remained poorly documented and completely unknown for Mexico until now.

Altogether our observations add to a growing body of evidence that TI is both widespread and highly variable among Auchenorrhyncha and Insecta in general. The precise case of *H. ichthyocephala* stands for its repeatability, clarity of its behavioral phases, and its documentation within a group largely overlooked in behavioral studies. By observing the phase-based model of TI in leafhoppers, we not only fill a significant gap in Hemipteran bioethology but also lay the groundwork for future research into the ecological and evolutionary drivers of antipredator behavior in insects.

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APÉNDICE

Supplementary material 1. Video of *Osbornellus* sp. (Hemiptera, Cicadellidae) at Mexico City: https://www.youtube.com/watch?v=vg_Fab7PBX0

Supplementary material 2. Video of *Homalodisca ichthyocephala* (Signoret, 1854) (Hemiptera, Cicadellidae) at Zirándaro, Mexico.
https://www.youtube.com/watch?v=GPG1DQHMNQ0