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Intake of Plant Resin Through the Genitalia of Two Asian Assassin Bugs (Reduviidae: Harpactorinae: Harpactorini)

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Abstract Many insects use tactics to protect their eggs from predation, infection, and water loss, among other risks. Some assassin bugs only in the New World tribe Apiomerini are known to use plant substances, such as resin, instead of secretions to protect their eggs. Here, we report a novel storage mechanism and the utilization of plant resin for egg protection in Asian assassin bugs, *Velinus nodipes* and *Agriosphodrus dohrni* (tribe: Harpactorini). Adult females of both species were observed to take in plant resin through their genitalia. We reported on the handling of resin by these species and confirmed that *A. dohrni* adult females stored resin in their subrectal glands and that the substance covering their egg masses was derived from plant resin. This is the first report on the storage of plant resin inside the bodies of assassin bugs and on resin-protected eggs in Harpactorini. Such internal resin storage was not accompanied by external morphological features, as observed in some Apiomerini assassin bugs, thereby suggesting that this tactic has been overlooked and may have evolved in broader tribes of assassin bugs than previously thought.

Keywords Egg-protecting tactics · body storage of resin · subrectal gland · *Velinus nodipes* · *Agriosphodrus dohrni*

Introduction

Some insect species, such as eusocial insects and some shield bugs, water bugs, and earwigs, directly and devotedly tend to and protect their eggs (i.e., show parental care, Vancassel 1984; Tallamy and Wood 1986; Tallamy 2001; Hanelová and Vilímová 2013). Although many other insects abandon their eggs without direct care, they protect their eggs by selecting suitable oviposition sites (Růžička 2001; Randlkofer et al. 2007; Sadek et al. 2010), applying defensive chemicals to them (Blum and Hilker 2008), encasing them in hardened structures (i.e., oothecae, Grimaldi and Engel 2005), and covering them with feces (e.g., chrysomelid beetles, Damman and Cappuccino 1991) and scales (e.g., lepidopteran species, Floater 1998). Such egg protection tactics are important for species survival because the egg stage is particularly vulnerable to natural enemies and environmental conditions (Hilker 1994).

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Many species of assassin bugs in Harpactorinae, a subfamily of Reduviidae, lay eggs in a single cluster on vegetation and cover these egg masses with frothy or gluey secretions termed spumaline (Kershaw 1909; Cobben and Wygodzinsky 1975; George 1988; Ambrose 1999). This egg-coating substance is hygroscopic (Salkeld 1972) and functions as a humidity regulator (Hinton 1961) that also protects the eggs from parasitoids (Swadener and Yonke 1973a, b; George 1988). Spumaline is secreted by and stored in the subrectal glands of Harpactorini, Diaspidini, and Tegeini [these tribes are suggested to be polyphyletic (Zhang et al. 2016)], whereas a few exceptions in these tribes and other harpactorine assassin bugs, such as Apiomerini and Ectinoderini, do not have such glands (Davis 1969; George 1988; Weirauch 2008).

Several species of Apiomerini use sticky plant substances, such as resins and trichome secretions, as defensive substances to protect their eggs and as adhesives to trap prey species. Instead of secreting spumaline, *Apiomerus flaviventris* adult females collect plant resins with their forelegs and then transfer these resins to the ventral surface of their abdomens where they are stored in long and dense setae. During oviposition, the females transfer the stored resins to the genital sclerites using the metatibial comb of their hindlegs, cover each egg with the resin immediately after exiting the genital opening, and then place each egg next to the other already deposited eggs to form an egg mass (Eisner 1988; Choe and Rust 2007; Forero et al. 2011). These plant resins protect the egg masses from desiccation and natural enemies, such as parasitoids and ants (Southwood 1956; Aldrich 1988; Wolf and Reid 2001). The stickiness and chemical composition of resins have been suggested to deter these enemies (Choe and Rust 2007). Additionally, the resins used to encase eggs provide the hatching immatures with an initial sticky trap to capture prey (Forero et al. 2011). In another Apiomerini member, *Heniartes stali*, plant trichome secretions are stored on the surface of its metatibiae and used to cover its eggs (Avila-Núñez et al. 2016).

Such resin based egg protection tactics have only been reported in the New World tribe Apiomerini (Forero and Weirauch 2016); however, even in tribes other than Apiomerini, species that use sticky traps derived from plant substances are likely to have evolved plant substance-based egg protection. Zhang et al. (2016) reported that the use of sticky traps evolved at least seven times in assassin bugs, once in the Apiomerini + Bactrodinae clade and the other six times in other harpactorine tribes. Members from one harpactorine lineage, including those from the genus *Zelus*, secrete sticky substances (Weirauch 2006; Zhang and Weirauch 2013). In the remaining five harpactorine lineages, which belong to Ectinoderini, Diaspidiini, and Harpactorini, plant resins or trichome secretions are used as sticky traps (Miller 1942; Usinger 1958; Zhang et al. 2016). However, the use of plant substances for egg protection has not been reported in these lineages. The resin-based egg protection tactic in assassin bugs other than Apiomerini may have been overlooked due to the lack of natural history studies.

Two species of Harpactorini, *Agriosphodrus dohrni* and *Velinus nodipes*, are often found on pine trees that frequently exude resin (Inoue 1988; Ishikawa et al. 2012). *Agriosphodrus dohrni* is naturally distributed in India, Indochina, and China, and was accidentally introduced to Japan, while *V. nodipes* is naturally distributed in China, Korea, and Japan (Ishikawa et al. 2012). *Agriosphodrus dohrni* is a univoltine species that overwinters in its fifth instar, develops to the adult stage in spring, and then mates and lays eggs in late spring to early summer (Luo et al. 2010; Naito 2017). Female *A. dohrni* cover their egg masses with copious secretions (Luo et al. 2010). Although information on the life history of *V. nodipes* is very limited, this species is known to overwinter in its fifth instar (Naito 2017) and it is probably a univoltine species. The Japanese name of *V. nodipes*, Yani-sashigame, means “resin assassin bug” and it is known to cover its body with plant resin and to utilize this resin to capture prey (Naito 2017). Therefore, if *A. dohrni* and *V. nodipes* also display the resin based egg protection tactic, this tactic may have evolved in assassin bugs other than Apiomerini and in broader taxa in Reduviidae than previously thought.

In the present study, we investigated if *A. dohrni* and *V. nodipes* utilize plant resins to cover their eggs and found that both species displayed resin-collecting and resin storage behaviors that differed from those of Apiomerini assassin bugs. By providing colored resin to females under laboratory conditions, we were able to detect the resin storage location. Furthermore, thin layer chromatography enabled the comparison of the plant resin, stored resin, and egg-coating substance to clarify the origin of the stored resin and if the stored resin was used by the assassin bugs as an egg-coating substance.

Materials and Methods

Insect Collection and Rearing

We collected 22 *A. dohrni* females, including 10 fifth (last) instar juveniles and 12 adults, from Japanese cherry trees *Cerasus* × *yedoensis* and 2 *V. nodipes* adult females from a Japanese fir *Abies firma* and a Japanese cedar *Cryptomeria japonica*, all in the Kyoto Prefecture, Japan. The 10 juvenile *A. dohrni* females were reared until the adult stage in individual plastic cups (100 × 95 mm, diameter × depth), each containing a folded filter paper on the bottom and a water-soaked Kim Wipe for drinking and moisture. After reaching the adult stage, these 10 females were used for behavioral observations and subsequent experimentation and analysis. The two *A. dohrni* adult females and two *V. nodipes* adult females captured in the field were also maintained under the same conditions until oviposition. All insects were fed three chopped *Tenebrio molitor* mealworms every 2 or 3 days, and were maintained in climate-controlled rooms at 25 ± 2 °C and under a 16:8 light/dark photoperiod. The remaining 10 *A. dohrni* adult females captured in the field were dissected to obtain the subrectal glands for silica gel thin layer chromatography (TLC) analysis. Table 1 lists all protocols used in the present study, relative to the study individuals.

Resin Collection, Intake, and Internal Storage

The resin collection behavior of *V. nodipes* was observed on a Japanese fir tree and that of *A. dohrni* was observed on a *Pinus thunbergii* (Japanese black pine) tree in the field. Of the two *V. nodipes* adults caught in the field, one was the individual whose behavior we observed. Both adults were maintained under laboratory conditions until oviposition. To identify the storage location of the collected resin, we mixed a synthetic resin (Canada balsam, Sigma-Aldrich) with blue coloring and presented this colored resin (on the folded filter paper) to each of the 10 *A. dohrni* adult females that had been reared from the fifth instar in the individual plastic cups. After observing their resin-collecting behavior, we retained 1 of the 10 *A. dohrni* until oviposition to confirm if the colored resin was used to cover its egg mass, and dissected the remaining 9 individuals to identify the storage location of the colored resin.

Identification of Resin Source Plants and Egg-coating Substances

We conducted silica gel TLC to examine which substances adult *A. dohrni* females utilize under natural conditions. Specifically, the TLC was performed on the egg masses laid by 2 of the 12 adult females captured in the field and on the subrectal glands harvested from the remaining 10 *A. dohrni* adults. The pairs of subrectal glands from each *A. dohrni* adult female were extracted using 3 mL of 1,2-dichloroethane for 30 s; thus, a total of 10 subrectal gland extracts were obtained. The two egg masses were also extracted separately in the same way. Samples of each extract (3 μL) were spotted on a silica gel TLC plate, which was developed with hexane-ethyl acetate (2:1) and visualized with p-anisaldehyde stain (Touchstone 1992). We also compared the TLC spots of two plant substances: the resin of Japanese black pine and the sap of Japanese cherry tree, with the extracts from subrectal glands and egg masses of *A. dohrni* since individuals of this species were frequently observed on these trees. Additionally, TLC was performed for the eggs of *V. nodipes*, for the resin of Japanese fir, Japanese black pine, and Japanese cedar, and for the sap of the Japanese cherry tree.

Results

Resin-intake Behavior and Oviposition of *V. nodipes*

One *V. nodipes* adult female was observed directly on the stem of Japanese fir in the field. The tip of its abdomen was attached to the plant resin, and it was observed to repeatedly open and shut the abdomen tip to move the resin into its body (Fig. 1a, b, Movie S1). This *V. nodipes* female laid 16 eggs in the rearing plastic cup, of which 12 formed a mass and 4 were laid separately. Another *V. nodipes* caught on Japanese cedar laid three eggs which were not clustered together. All eggs were coated with a transparent substance (Fig. 1c).

Resin-intake behavior and resin storage locations in *A. dohrni*

The single *A. dohrni* adult female that was collected and observed to take up Japanese black pine resin in the field showed identical resin-intake behavior to that of the 10

Table 1 Overview of the experimental protocols and data collection used for the assassin bugs in the present study

Species	Collection stage	Number of specimens	Treatments				
			Laboratory rearing	Harvesting of subrectal glands for TLC	Behavioral observation for colored resin	Dissection for resin storage location within the body	Obtained eggs
Agriosphodrus dohrni	fifth instar juvenile	9	+		+	+	
		1	+		+		+
	adult	10		+			
		2	+				+
Velinus nodipes	adult	2	+				+

"+" indicates that the treatment was applied to the specimens. TLC, thin layer chromatography

laboratory-reared *A. dohrni* adult females presented with the colored Canada balsam (Fig. 2, Movie S2). However, the collection process differed from that for *V. nodipes*. Adult *A. dohrni* females collected dabs of resin with the tarsi of their forelegs (Fig. 2a) and applied it to the femurs of their midlegs (Fig. 2b). After repeating this sequential behavior several times, the resin on the midleg femurs was then transferred to the tip of the abdomen using the tibiae of the hindlegs (Fig. 2c,d) and moved into the body by repeatedly opening and shutting the abdomen tip (Fig. 2e). All 10 *A. dohrni* females showed this sequential behavior and took up the colored Canada balsam. Dissection of the 9 *A. dohrni* adults revealed that they stored the resin in their subrectal glands (Fig. 2f). The remaining adult female laid eggs and covered them with the colored resin, 7 days after collection and storage in its body (Fig. 2g).

Identification of Resin Source Plants and Egg-coating Substances

Of the 10 dissected *A. dohrni* adult females collected in the field, 6 showed filled subrectal glands and 4 showed empty subrectal glands. The extracts of the 6 filled subrectal glands showed almost identical spot patterns, and were similar to those of the pine resin and egg masses of *A. dohrni* (Fig. 3a). However, the color of the spots of egg mass extracts, which were blue-purple, differed from the color of the other spots, which were red-purple. The extracts of cherry sap and empty subrectal glands showed no spots (Fig. 3a). The two extracts of the egg masses of *V. nodipes* showed different spot patterns. The extracts of the *V. nodipes* that took up resin from the fir tree showed the same pattern as the extract of fir resin, and the extract of the *V. nodipes*

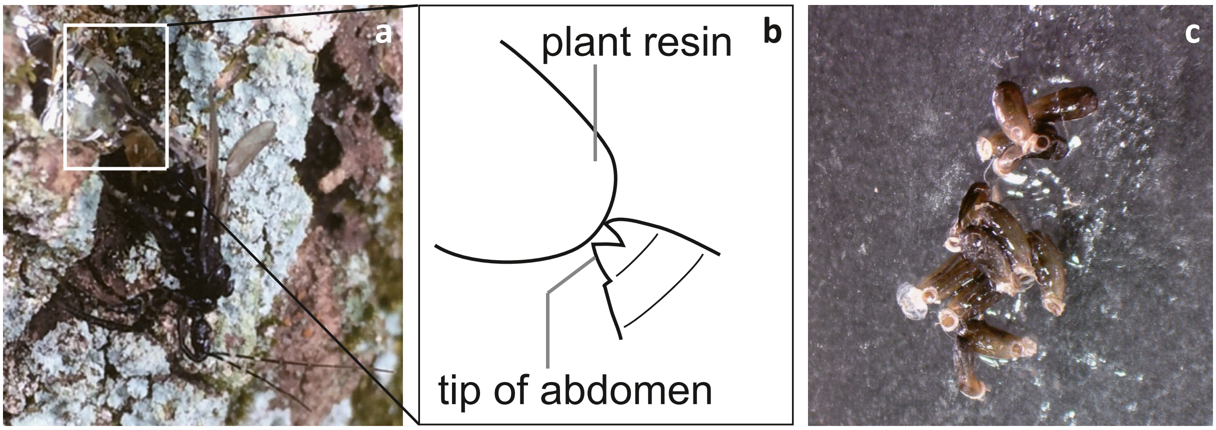

Fig. 1 Resin-intake behavior and a coated egg mass of *Velinus nodipes*. Adult *V. nodipes* female taking up resin (**a**). Abdomen tip of adult *V. nodipes* (**b**). Egg mass coated with a transparent resin-like substance (**c**)

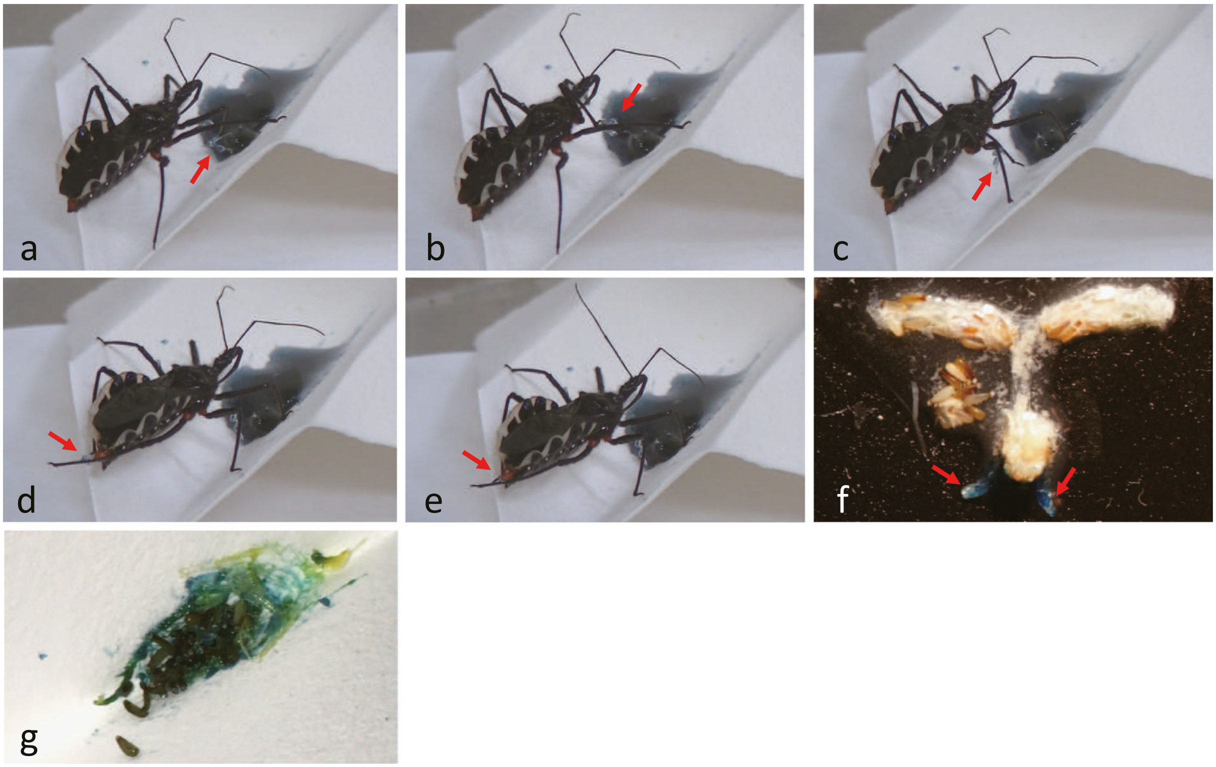

Fig. 2 Sequential resin-intaking behavior, colored resin stored in subrectal glands, and colored resin-coated egg mass of *Agriosphodrus dohrni*. The adult *A. dohrni* female collected the blue colored resin with the tarsus of its foreleg (**a**), applied it to the femur of its midleg (**b**), then used the tibia of its hindleg (**c**) to transfer the resin to the tip of the abdomen (**d**). Finally, the resin was taken up into its body (**e**). The transferred resin is indicated by arrows. Isolated reproductive organs and subrectal glands containing the blue colored resin (**f**; arrows). Egg mass laid by a female that took up the blue colored resin (**g**)

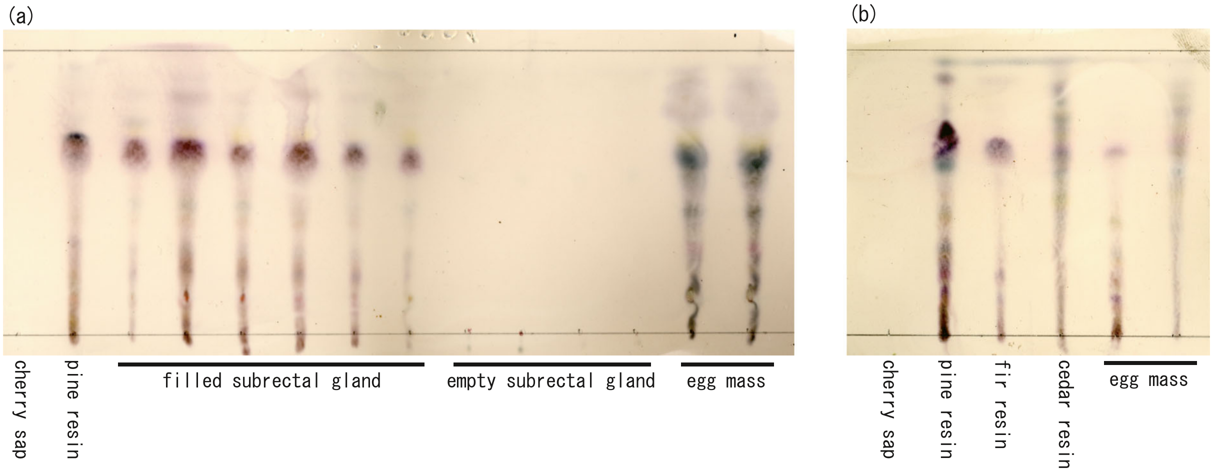

Fig. 3 Spot patterns of egg masses and subrectal glands of *Agriosphodrus dohrni* and *Velinus nodipes* on thin layer chromatography (TLC). Spot patterns of the extracts of six filled subrectal glands, four empty subrectal glands, and two egg masses of *A. dohrni* on a TLC plate with extracts of cherry tree sap and pine tree resin (**a**). Spot patterns of the extracts of the two egg masses of *V. nodipes*, cherry tree sap, pine tree, fir, and cedar resins applied on the other TLC plate (**b**)

collected from a Japanese cedar showed the same pattern as the extract of cedar resin (Fig. 3b).

Discussion

The present study revealed that *A. dohrni* and *V. nodipes* took up tree resin through their genitalia. In addition, *A. dohrni* was shown to store tree resin in its subrectal glands and then use the resin to cover its egg masses. The TLC analysis confirmed that the egg coating substances of both species were derived from plant resins. This is the first report on the utilization of plant resins by Harpactorini assassin bugs for egg protection, and the uptake and storage of resin within the body of Reduviidae. Egg protection tactics have only been reported for the New World Apiomerini, where egg coating behavior with resin was suggested to evolve in the last common ancestor of the Apiomerus suprageneric clade (Forero and Weirauch 2016) and egg coating behavior with trichome secretion was reported in *H. stali*, which belongs to the Heniartes suprageneric clade (Avila-Núñez et al. 2016). Furthermore, this study demonstrated the use of plant substances-based egg protection in two additional species of Harpactorini assassin bugs. This suggests egg protection using plant-derived sticky substances may be a more common tactic among a diverse array of lineages than previously thought; at least within the Harpactorinae.

The TLC analysis also revealed that the two *V. nodipes* adult females used the resin of the trees from which they were collected; one used resin from Japanese fir and the other used resin from Japanese cedar. Some of the eggs that were oviposited were not clustered, which may have been due to rearing conditions not being optimal for oviposition. According to the TLC analysis, *A. dohrni* uses pine resin, although we collected *A. dohrni* from cherry trees and not from pine trees. In addition, spot colors differed between filled subrectal glands and egg masses. All spots were originally blue-purple when we conducted the TLC analysis just after extraction (Figure S1). However, spot color of pine resin and filled subrectal glands changed from blue-purple to red-purple, probably due to the long storage period, whereas spot color of the *A dohrni* egg masses remained blue-purple. We, therefore, hypothesized that *A. dohrni* might add secretions to the stored resin that prevents its color from changing, which is supported by *A. dohrni* taking up transparent resin but presenting yellowish-covered egg masses (Luo et al. 2010).

It is unknown whether the resin based egg protection tactic of *A. dohrni* and *V. nodipes* evolved independently or was derived from a common ancestor. These two Harpactorini are relatively closely related, and belong to the same clade in Harpactorini (Zhang et al. 2016). In this clade, the genera *Sinea* and *Irantha* lack subrectal glands (Davis 1969; George 1988) whereas another species, *Sycanus croceovittatus*, reportedly covers its egg mass with a large amount of sticky substance (Huang et al. 1991). The presence of subrectal glands is thought to be apomorphic character as they are found in many species of Harpactorinae (Davis 1969). This suggests that the absence of subrectal glands in genera *Sinea* and *Irantha* may be a result of the loss of this trait. However, it is unknown whether egg protecting substances of other species are secretions or plant-derived. Additional investigations are needed to determine the source of egg protecting substances to reveal which functions of subrectal glands are ancestral and commonly distributed in the Harpactorini, to secrete egg protecting substances or to store plant-derived substances.

Forero and Weirauch (2016) suggested that Apiomerini members, which utilize plant resins for maternal care, have certain external features, such as dense and long setation of sternites (used for storing resin) and a metatibial comb on their hindlegs (used to apply stored resin to the eggs during oviposition). Such external features of Apiomerini might have evolved due to the lack of subrectal glands (Davis 1969; Weirauch 2008). On the other hand, the two Harpactorini species in the present study do not exhibit such external features, and instead stored resin in the subrectal glands located near the genital opening which enable them to cover the eggs with resin without using hindlegs. In fact, *A. dohrni* does not use its hindlegs for oviposition (Luo et al. 2010). This is required to directly observe the resin-intake behavior of Harpactorini, or compare the egg-coating substances with plant substances via chemical analysis, to confirm if these assassin bugs covered their eggs with plant substances or secretions.

Overall, the present study revealed that two species of Asian assassin bugs stored plant resins in their bodies and subsequently used it to cover their egg masses. Such resin based egg protection tactics might be used by other species of harpactorine assassin bugs and in broader taxa in Reduviidae than previously thought. However, such tactics may have been overlooked because the internal resin storage feature of these assassin bugs is not accompanied by external features, such as abdominal setation and a metatibial comb. It is likely that plant substance-based egg protection occurs more frequently in species that use plant substances as sticky traps. In fact, all Apiomerini species that protect their egg masses with plant substances use sticky traps (Forero et al. 2011; Avila-Núñez et al. 2016) and *V. nodipes* also uses resin as sticky traps (Naito 2017). However, resin-based egg protection can also be used by species that do not construct sticky traps as observed in *A. dohrni*.

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Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

Code Availability No software application or custom code are used in this study.

References

Aldrich JR (1988) Chemical ecology of the heteroptera. Annu Rev Entomol 33:211–238. https://doi.org/10.1146/annurev.en.33.010188.001235

Ambrose DP (1999) Oviposition behaviour. Assassin bugs. Science Publishers Inc., Enfield, pp 202–206

Avila-Núñez JL, Naya M, Otero LD, Alonso-Amelot ME (2016) A resin bug (Reduviidae: Harpactorinae: Apiomerini) harvesting the trichome secretion from an Andean blackberry. Neotrop Biodivers 2:151–158. https://doi.org/10.1080/23766808.2016.1240061

Blum MS, Hilker M (2008) Chemical protection of insect eggs. In: Hilker M, Meiners T (eds) Chemoecology of Insect Eggs and Egg Deposition. Blackwell, Berlin, pp 61–90

Choe D-H, Rust MK (2007) Use of plant resin by a bee assassin bug, *Apiomerus flaviventris* (Hemiptera: Reduviidae). Ann Entomol Soc Am 100:320–326. https://doi.org/10.1603/0013-8746(2007)100[320:UOPRBA]2.0.CO;2

Cobben R, Wygodzinsky PW (1975) The Heteroptera of the Netherlands antilles – IX Reduviidae (Assassin bugs). Stud Fauna Curaçao other Caribb Islands 48:1–62

Damman H, Cappuccino N (1991) Two forms of egg defence in a chrysomelid beetle: egg clumping and excrement cover. Ecol Entomol 16:163–167. https://doi.org/10.1111/j.1365-2311.1991.tb00205.x

Davis NT (1969) Contribution to the morphology and phylogeny of the Reduvioidea. Part IV. The Harpactoroid complex. Ann Entomol Soc Am 62:74–94. https://doi.org/10.1093/aesa/62.1.74

Eisner T (1988) Insekten als fürsorgliche Eltern. Verh Dtsch Zool Ges 81:9–17

Floater GJ (1998) Tuft scales and egg protection in *Ochrogaster lunifer* Herrich-Schäffer (Lepidoptera: Thaumetopoeidae). Aust J Entomol Entomol 37:34–39. https://doi.org/10.1111/j.1440-6055.1998.tb01540.x

Forero D, Weirauch C (2016) Resin-enabled maternal care is an old evolutionary strategy in New World resin bugs (Hemiptera: Reduviidae). Zool J Linn Soc 179:62–91. https://doi.org/10.1111/zoj.12454

Forero D, Choe DH, Weirauch C (2011) Resin gathering in neotropical resin bugs (Insecta: Hemiptera: Reduviidae): Functional and comparative morphology. J Morphol 272:204–229. https://doi.org/10.1002/jmor.10907

George AR (1988) Subrectal glands of Reduviidae (Insecta-Heteroptera). Proc Anim Sci 97:211–222. https://doi.org/10.1007/BF03179531

Grimaldi D, Engel MS (2005) Evolution of the Insects. Cambridge University Press, Cambridge

Hanelová J, Vilímová J (2013) Behaviour of the central European Acanthosomatidae (Hemiptera: Heteroptera: Pentatomoidea) during oviposition and parental care. Sci Biol 98:433–457

Hilker M (1994) Egg deposition and protection of eggs in Chrysomelidae. In: Jolivet PH, Cox ML, Petitpierre E (eds) Novel aspects of the biology of Chrysomelidae. Springer, Berlin, pp 263–276

Hinton HE (1961) The structure and function of the egg-shell in the Nepidae (Hemiptera). J Insect Physiol 7:224–234. https://doi.org/10.1016/0022-1910(61)90075-0

Huang Z, Wu J, Zhang Z (1991) A preliminary study on the bionomics and application of *Sycanus croceovittatus* (Hemiptera, Reduviidae). For Res 4:57–64

Inoue H (1988) Food availability and reproductive performance in the predator, *Agriosphodrus dohrni* signoret (Hemiptera: Reduviidae): Is its population food-limited in the field? Res Popul Ecol (Kyoto) 30:95–105. https://doi.org/10.1007/BF02512605

Ishikawa T, Takai M, Yasunaga T (2012) A field guide to Japanese bugs -Terrestrial Heteropterans-, vol 3. Zenkoku Noson Kyoiku Kyokai, Publishing Co., Ltd., Tokyo

Kershaw JCW (1909) On the metamorphoses and anatomy of the reduviid bug *Sycanus croceovittatus* Dohrn. Ann la Socit Entomol Belgique 53:241–249

Luo X, Zhou D, Li H et al (2010) Taxonomic and bionomic notes on *Agriosphodrus dohrni* (Signoret) (Hemiptera: Reduviidae: Harpactorinae). Zootaxa 2358:57–67. https://doi.org/10.5281/zenodo.193604

Miller NCE (1942) On the structure of the legs in Reduviidae (Rhynchota). Proc R Entomol Soc London, Ser A. Gen Entomol 17:49–58

Naito M (2017) Insect fauna around Higashiyama in Nagoya III. Hemiptera (2) Reduviidae, Coreidae, etc. Treatise Collect Sugiyama Jogakuen Univ 48:137–148

Randlkofer B, Obermaier E, Meiners T (2007) Mother's choice of the oviposition site: Balancing risk of egg parasitism and need of food supply for the progeny with an infochemical shelter? Chemoecology 17:177–186. https://doi.org/10.1007/s00049-007-0377-9

Růžička Z (2001) Oviposition responses of *aphidophagous coccinellids* to tracks of ladybird (Coleoptera: Coccinellidae) and lacewing (Neuroptera: Chrysopidae) larvae. Eur J Entomol 98:183–188. https://doi.org/10.14411/eje.2001.034

Sadek MM, Hansson BS, Anderson P (2010) Does risk of egg parasitism affect choice of oviposition sites by a moth? A field and laboratory study. Basic Appl Ecol 11:135–143. https://doi.org/10.1016/j.baae.2009.09.003

Salkeld EH (1972) The chorionic architecture of *Zelus exsanguis* (Hemiptera: Reduviidae). Can Entomol 104:433–442. https://doi.org/10.4039/Ent104433-3

Southwood TRE (1956) The structure of the eggs of the terrestrial Heteroptera and its relationship to the classification of the group. Ecol Entomol 108:163–221. https://doi.org/10.1111/j.1365-2311.1956.tb02269.x

Swadener SO, Yonke TR (1973a) Immature stages and biology of *Apiomerus crassipes* (Hemiptera: Reduviidae). Ann Entomol Soc Am 66:188–196. https://doi.org/10.1093/aesa/66.1.188

Swadener SO, Yonke TR (1973b) Immature stages and biology of *Zelus socius* (Hemiptera: Reduviidae). Can Entomol 105:231–238. https://doi.org/10.4039/Ent105231-2

Tallamy DW (2001) Evolution of exclusive paternal care in arthropods. Annu Rev Entomol 46:139–165. https://doi.org/10.1002/9783527678679.dg04082

Tallamy DW, Wood TK (1986) Convergence patterns in subsocial insects. Annu Rev Entomol 31:369–390. https://doi.org/10.1146/annurev.ento.31.1.369

Touchstone JC (1992) Practice of thin layer chromatography. Wiley, Hoboken

Usinger RL (1958) The Pan-Pacific entomologist. Pan-Pac Entomol 34:52

Vancassel M (1984) Plasticity and adaptive radiation of dermapteran parental behavior: results and perspectives. In: Advances in the Study of Behavior. Elsevier, Amsterdam, pp 51–80

Weirauch C (2006) Observations on the sticky trap predator *Zelus luridus* Stål (Heteroptera, Reduviidae, Harpactorinae), with the description of a novel gland associated with the female genitalia. Denisia 19:1169–1180

Weirauch C (2008) Cladistic analysis of Reduviidae (Heteroptera: Cimicomorpha) based on morphological characters. Syst Entomol 33:229–274. https://doi.org/10.1111/j.1365-3113.2007.00417.x

Wolf KW, Reid W (2001) Surface morphology of legs in the assassin bug *Zelus longipes* (Hemiptera: Reduviidae): a scanning electron microscopy study with an emphasis on hairs and pores. Ann Entomol Soc Am 94:457–461. https://doi.org/10.1603/0013-8746(2001)094

Zhang G, Weirauch C (2013) Sticky predators: a comparative study of sticky glands in harpactorine assassin bugs (Insecta : Hemiptera : Reduviidae). Acta Zool 94:1–10. https://doi.org/10.1111/j.1463-6395.2011.00522.x

Zhang J, Weirauch C, Zhang G, Forero D (2016) Molecular phylogeny of Harpactorinae and Bactrodinae uncovers complex evolution of sticky trap predation in assassin bugs (Heteroptera: Reduviidae). Cladistics 32:538–554. https://doi.org/10.1111/cla.12140