



Short Communication

Maternal care in *Gargaphia decoris* (Heteroptera, Tingidae),
with comments on this behavior within the genus and family



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ARTICLE INFO

Article history:

Received 21 August 2014

Accepted 9 February 2015

Available online 9 April 2015

Associate Editor: Kleber Del Claro

ABSTRACT

Maternal care in *Gargaphia decoris* is described for the first time. A video is presented as supplementary material. The knowledge on such trait within Tingidae is summarized. The behavior within the family is discussed, and the potential as a source of phylogenetic characters for further analyses is stressed.

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Keywords:

Gargaphia

Neotropical

Parental care

Solanum concinnum

Maternal care in Tingidae was first reported for *Gargaphia tiliae* (Walsh, 1864) (Weiss, 1919) and since then just a few additional species have been observed with this rare behavior. Besides *G. tiliae*, there are records of maternal care for six other species distributed in three other genera, two from the New World and one from Africa. Within *Gargaphia* Stål, *G. solani* Heidemann, 1914, *G. iridescent* Champion, 1897 and *G. decoris* Drake, 1931 also present this trait (Fink, 1915; Torre-Bueno, 1942; Olckers, 2000). Other taxa exhibiting maternal care are *Corythucha bulbosa* Osborn and Drake, 1916 (Sheeley and Yonke, 1977), *C. hewitti* Drake, 1919 (Faeth, 1989) and *Leptobyrsa decora* Drake, 1922 (Melksham, 1984) in the New World and *Compseuta picta* Schouteden, 1923 (Tallamy and Igay, 2004) in Africa. A complete list of references treating this subject in Tingidae is provided (Table 1). There are several differences in how maternal care is expressed among these taxa. Egg-dumping, egg-guarding, colonial oviposition, and aggressive defense against predators have all been reported in various combinations within Tingidae.

Leptobyrsa decora is a Neotropical species, which presents colonial oviposition and egg-guarding. Females remain with immatures until the fourth instar (Melksham, 1984). Loeb and Bell (2006) suggested that cooperation between females with the task of egg-guarding is controlled by chemical cues and not physical cohesion among partners. Melksham (1984) showed differences in the

number of egg batches and adult guards between two different populations of this lace bug. This may be correlated with unequal predation pressure. Still, according to Melksham (1984), wing-fanning was observed in this species but the context of this behavior was not defined. Within the genus *Corythucha*, maternal care has been observed in two species (Sheeley and Yonke, 1977; Faeth, 1989), but this behavior apparently is absent in several others (Tallamy and Denno, 1981b). Faeth (1989) observed egg-guarding in *C. hewitti*, but not aggressive brood protection. Females seem to communicate with their young through chemicals dispersed from abdominal movements. This communication may regulate nymphal aggregation, offering protection from the dilution effect of predation or it may be a mechanism to guide nymphal movements (Faeth, 1989). In addition to egg-guarding, wing-fanning was observed in *Corythucha bulbosa* against a spider (Sheeley and Yonke, 1977). *Compseuta picta*, the first tingid outside the New World in which maternal care has been recognized, presented egg-guarding and wing-fanning every time an inanimate aggressor approached its eggs or nymphs (Tallamy and Igay, 2004). The experiments with these females were interrupted due to time constraints, but females remained with and defended their offspring throughout the two days of observation (Tallamy and Igay, 2004).

Two alternative reproductive strategies have been observed in the *Gargaphia* species cited above: egg-dumping and egg-guarding. Although these strategies have been better studied in *G. solani* and *G. tiliae*, *G. iridescent* also exhibits these behaviors (Torre-Bueno, 1935; Tallamy, 2005). Egg dumping is analogous to the avian

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Table 1

List of references on maternal care behavior in Tingidae.

Species	Reference
<i>Compseuta picta</i>	Tallamy and Igley (2004)
<i>Corythucha bulbosa</i>	Sheehey and Yonke (1977)
<i>Corythucha hewitti</i>	Faeth (1989)
<i>Gargaphia decoris</i>	Olckers (2000)
<i>Gargaphia iridescens</i>	Tallamy (2005)
<i>Gargaphia solani</i>	Fink (1915)
	Kearns and Yamamoto (1981)
	Tallamy and Denno (1981a)
	Tallamy and Denno (1981b)
	Tallamy (1982)
	Tallamy and Denno (1982)
	Tallamy (1985)
	Tallamy (1986)
	Hardin and Tallamy (1992)
	Tallamy and Tallamy (1993)
	Monaco et al. (1998)
	Loeb et al. (2000)
	Tallamy et al. (2002)
	Parr et al. (2002)
	Loeb (2003)
	Weiss (1919)
<i>Gargaphia tiliae</i>	Torre-Bueno (1935)
<i>Leptobyrsa decora</i>	Hardin and Tallamy (1992)
	Melksham (1984)
	Loeb and Bell (2006)

behavior of certain taxa which regularly or occasionally lay eggs in the nests of conspecifics (Tallamy, 2005). Maternal *Gargaphia* are not the only invertebrates to exhibit conspecific egg-dumping, this behavior also has been recognized in subsocial bees and wasps (e.g., Brockmann, 1993) and treehoppers (Eberhard, 1986; Zink, 2003). Once physiologically committed to egg-guarding, a female protects eggs and nymphs under her care by offensively moving toward the predator while wing-fanning, sometimes even climbing on the top of the predator (Tallamy and Denno, 1981a). Egg-dumpers, in contrast, abandon their eggs to the care of egg-guarders and go off to produce more eggs elsewhere. In this way egg-dumpers can produce more than twice as many eggs as egg-guarders in their lifetime (Tallamy and Horton, 1990; Tallamy, 2005). Egg-guarders suspend further egg production until their first clutch reaches adulthood and independence (Tallamy and Denno, 1982).

Rather than being victims of egg-dumpers, egg-guarders benefit from receiving dumper eggs because they are typically laid around the perimeter of the guarder's egg mass, providing a buffer against incoming predators. This buffer dilutes losses of the guarding female's eggs and nymphs (Tallamy and Horton, 1990). Whenever possible, females dump their eggs instead of caring for their brood, since the egg-dumping strategy yields more eggs and avoids the hazards associated with predator encounters (Monaco et al., 1998). When a suitable egg mass is not available for would be egg-dumpers, gravid females lay and care for their own eggs. The egg-guarding/egg-dumping alternatives are controlled by juvenile hormone (JH); high levels of JH promote egg-dumping behavior and low levels trigger egg-guarding (Tallamy et al., 2002). The relationship between maternal alternatives and JH in *Gargaphia* lacebugs is consistent with other demonstrated roles of JH in parental care, vitellogenesis, and oviposition (e.g., Martinez and Huerta, 1997; Rankin and Riddiford, 1977). The complex behavioral interactions between egg-dumpers and egg-guarders have been extensively studied in *G. solani* in which trade-offs, proximate regulation, chemical mediation, egg-mass recognition and relatedness were explored (Tallamy and Denno, 1981a, 1982; Tallamy and Tallamy, 1993; Monaco et al., 1998; Loeb et al., 2000; Parr et al., 2002).

In July 2013, females of *Gargaphia decoris* presenting egg-guarding behavior were observed (Fig. 1). We found this species in



Fig. 1. *Gargaphia decoris* Drake, 1931 female guarding an egg batch with first instar nymphs. Scale bar: 1 mm. Photo: Marsaro Júnior, A.L.

the municipality of Passo Fundo, Rio Grande do Sul, Brazil ($28^{\circ}13' S$, $52^{\circ}24' W$), on the abaxial surface of leaves of *Solanum concinnum* (Solanaceae). Vouchers were deposited in the Museu de Ciências Naturais of Fundação Zoobotânica do Rio Grande do Sul (MCNZ), in Porto Alegre, Rio Grande do Sul. Four leaves, three containing a guard female with eggs, and one containing a female with eggs hatching to first instar nymphs, were collected for preliminary laboratory tests. Under a stereomicroscope, we disturbed the female with a needle, touching her sides and advancing toward the egg batch in front of her. These tests were filmed, and a video is available as supplementary material (Guidoti et al., 2015). The wing-fanning behavior was observed only for the female guarding both eggs and nymphs. When disturbed on the side of the body, the female just moved a little, returning to the guard position right after the needle was withdrawn. When disturbed by frontal movements in direction of the egg batch, the female moved aggressively toward the needle. The female fanned her wings only after she charged the needle. Further studies were not possible due a cold wave that substantially reduced the populations of this lace bug. Olckers (2000) reported but did not describe maternal care for *G. decoris*; our description now provides details that suggest maternal care in *G. decoris* is similar to that described in other species of *Gargaphia* thus far. More experiments are needed to fully characterize the behavior in *G. decoris*.

Gargaphia, as it is currently defined, is a New World genus comprising about 70 species, but it lacks a phylogenetic hypothesis designed specifically to test its monophyly. Recently, *G. arizonica* Drake and Carvalho, 1944, *G. tiliae* and *G. solani* were included in a molecular phylogenetic analysis, supporting the monophyly of the genus (Guilbert et al., 2014). However, an unpublished thesis suggests *Gargaphia* should be divided into several distinct genera (Smith, 1996). Although the aforementioned *Gargaphia* species exhibit maternal care with the exception of *G. arizonica* (Hardin and Tallamy, 1992), these four species are both morphologically and behaviorally similar, and therefore we suggest that maternal care could be a defining trait of a single subsection of *Gargaphia*. Thus, the behavior could be included as character for future phylogenetic analyses of this group.

The fact that different expressions of maternal care have been observed in Tingidae enhances the evolutionary questions regarding this trait in the family. Even though we expect that maternal care has evolved in more Tingidae species than is currently recognized (Tallamy and Igley, 2004), it has still only been observed in a few species, indicating that Tingidae systematics could benefit from additional data on the presence or absence of brood protection across the family. Not only would genus-level systematics improve from the availability of such data, but additional behavioral descriptions would enable the testing of hypotheses about the evolution

of maternal care in Tingidae. Therefore, more attention should be given to this behavior in other Tingidae. We urge that such data should not be neglected and the presence or the absence of such trait should always be reported.

Conflicts of interest

The authors declare no conflicts of interest.

Acknowledgments

We thank Aline Barcellos, Carolina Adami and Filipe Michels for their comments on the first version of this manuscript. To Dennis Kopp, Eric Guilbert Joe Eger, Randall Schuh and Thomas Henry, for their encouragements in publish this data. CNPq (Brazil) for the Master's Degree fellowship supporting the first author.

Appendix A. Supplementary data

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.rbe.2015.03.004.

References

- Brockmann, H.J., 1993. Parasitizing conspecifics: comparisons between hymenoptera and birds. *Trends Ecol. Evol.* 8, 2–4.
- Eberhard, W.G., 1986. Possible mutualism between females of the subsocial membracid *Polyglypta dispar* (Homoptera). *Behav. Ecol. Sociobiol.* 19, 447–453.
- Faeth, S.H., 1989. Maternal care in lace bug, *Corythucha hewitti* (Hemiptera: Tingidae). *Psyche* (Stuttg) 96, 101–110.
- Fink, D.E., 1915. The eggplant lace-bug. *Bull. U.S. Dep. Agric.* 239, 1–7.
- Guidoti, M., Tallamy, D.W., Marsaro Jr., A.L., 2015. Gargaphia decoris (Hemiptera, Tingidae) maternal care display. figshare. Available at: <http://dx.doi.org/10.6084/m9.figshare.1375660>. (accessed 13 April 2015).
- Guilbert, É., Damgaard, J., D'Haese, C.A., 2014. Phylogeny of the lacebugs (Insecta: Heteroptera: Tingidae) using morphological and molecular data. *Syst. Entomol.* 39, 431–441.
- Hardin, M.R., Tallamy, D.W., 1992. Effect of predators and host phenology on the maternal and reproductive behaviors of *Gargaphia* lace bugs (Hemiptera: Tingidae). *J. Insect Behav.* 5, 177–192.
- Kearns, R.S., Yamamoto, R.T., 1981. Maternal behavior and alarm response in the eggplant lace bug, *Gargaphia solani* Heidemann (Tingidae: Heteroptera). *Psyche* (Stuttg) 88, 215–230.
- Loeb, M.L.G., 2003. Evolution of egg dumping in a subsocial insect. *Am. Nat.* 161, 129–142.
- Loeb, M.L.G., Bell, L.K., 2006. Distribution of care-giving effort in a communally breeding lace bug: fair guarding without coercion. *J. Insect Behav.* 19, 19–30.
- Loeb, M.L.G., Diener, L.M., Pfennig, D.W., 2000. Egg-dumping lace bugs preferentially oviposit with kin. *Anim. Behav.* 59, 379–383.
- Martinez, M.I., Huerta, C., 1997. Coordinated activity of the ovary, pars intercerebralis and corpus allatum during the prenesting and nesting cycles of *Copris incertus* Say (Coleoptera: Scarabaeidae: Scarabaeinae). *Coleopts. Bull.* 51, 351–383.
- Melksham, J.A., 1984. Colonial oviposition and maternal care in two strains of *Lepidocyrtus decora* Drake (Hemiptera: Tingidae). *J. Aust. Entomol. Soc.* 23, 205–210.
- Monaco, E.L., Tallamy, D.W., Johnson, R.K., 1998. Chemical mediation of egg dumping in the lace bug *Gargaphia solani* Heidemann (Heteroptera: Tingidae). *Anim. Behav.* 56, 1491–1495.
- Olckers, T., 2000. Biology, host specificity and risk assessment of *Gargaphia decoris*, the first agent to be released in South Africa for the biological control of the invasive tree *Solanum mauritianum*. *BioControl* 45, 373–388.
- Parr, A., Tallamy, D.W., Monaco, E.L., Pesek, J.D., 2002. Proximate factors regulating maternal options in the eggplant lace bug, *Gargaphia solani* (Heteroptera: Tingidae). *J. Insect Behav.* 15, 495–511.
- Rankin, M.A., Riddiford, L.M., 1977. Hormonal control of migratory flight in *Oncopeltus fasciatus*: the effects of the corpora cardiaca, corpora allata and starvation on migration and reproduction. *Gen. Comp. Endocrinol.* 33, 309–321.
- Sheeley, R.D., Yonke, T.R., 1977. Biological notes on seven species of Missouri Tingids (Hemiptera: Tingidae). *J. Kansas Entomol. Soc.* 50, 342–356.
- Smith, R.M., (Thesis) 1996. Phylogenetic analysis and revision of *Gargaphia* (sensu lato) (Heteroptera: Tingidae) with descriptions of one new genus and three new species groups. Texas A&M University.
- Tallamy, D.W., 1982. Age specific maternal defense in *Gargaphia solani* (Hemiptera: Tingidae). *Behav. Ecol. Sociobiol.* 11, 7–11.
- Tallamy, D.W., 1985. "Egg dumping" in lace bugs (*Gargaphia solani*, Hemiptera: Tingidae). *Behav. Ecol. Sociobiol.* 17, 357–362.
- Tallamy, D.W., 1986. Age specificity of "egg dumping" in *Gargaphia solani* (Hemiptera: Tingidae). *Anim. Behav.* 34, 599–603.
- Tallamy, D.W., 2005. Egg dumping in insects. *Annu. Rev. Entomol.* 50, 347–370.
- Tallamy, D.W., Denno, R.F., 1981a. Maternal care in *Gargaphia solani* (Hemiptera: Tingidae). *Anim. Behav.* 29, 771–778.
- Tallamy, D.W., Denno, R.F., 1981b. Alternative life history patterns in risky environments: an example from lacebugs. In: Denno, R.F., Dingle, H. (Eds.), *Insect Life History Patterns: Habitat and Geographic Variation*. Springer-Verlag New York Inc., pp. 129–147.
- Tallamy, D.W., Denno, R.F., 1982. Life history trade-offs in *Gargaphia Solani* (Hemiptera: Tingidae): the cost of reproduction. *Ecology* 63, 616–620.
- Tallamy, D.W., Horton, L.A., 1990. Costs and benefits of the egg-dumping alternative in *Gargaphia* lace bugs (Hemiptera: Tingidae). *Anim. Behav.* 39, 352–359.
- Tallamy, C.D., Tallamy, D.W., 1993. The effect of relatedness on *Gargaphia* egg dumping behavior. *Anim. Behav.* 45, 1239–1241.
- Tallamy, D.W., Igley, R.B., 2004. Maternal care in *Compseuta picta*, an African lace bug (Heteroptera: Tingidae). *J. Insect Behav.* 17, 247–249.
- Tallamy, D.W., Monaco, E.L., Pesek, J.D., 2002. Hormonal control of egg dumping and guarding in the lace bug, *Gargaphia solani* (Hemiptera: Tingidae). *J. Insect Behav.* 15, 467–475.
- Torre-Bueno, J.R., 1935. Notes on *Gargaphia tiliae*. *Bull. Brooklyn Entomol. Soc.* 30, 78.
- Torre-Bueno, J.R., 1942. Maternal solicitude in *Gargaphia iridesces champion*. *Bull. Brooklyn Entomol. Soc.* 37, 131.
- Weiss, H.B., 1919. Notes on *Gargaphia tiliae* Walsh, the linden lace-bug. *Proc. Biol. Soc. Wash.* 32, 165–168.
- Zink, A.G., 2003. Intraspecific brood parasitism as a conditional reproductive tactic in the treehopper *Publilia concava*. *Behav. Ecol. Sociobiol.* 54, 406–415.