Maternal-care behaviour in *Adomerus variegatus* (Hemiptera: Cydnidae)

Hiromi Mukai[1]

Department of Applied Biological Sciences, Faculty of Agriculture, Saga University, Honjo 1, Saga 840-8502, Japan

Mantaro Hironaka

Department of Biology, Faculty of Medicine, Hamamatsu University School of Medicine, Handayama 1-20-1, Hamamatsu, Shizuoka 431-3192, Japan

Narumi Baba

Graduate School of Bioresources and Bioenvironmental Sciences, Kyushu University, Hakozaki 6-10-1, Higashi-ku, Fukuoka 812-8581, Japan

Takao Yanagi, Koichi Inadomi

Department of Applied Biological Sciences, Faculty of Agriculture, Saga University, Honjo 1, Saga 840-8502, Japan

Lisa Filippi

Department of Biology, Hofstra University, Hempstead, New York 11549, United States of America

Shintaro Nomakuchi

Department of Applied Biological Sciences, Faculty of Agriculture, Saga University, Honjo 1, Saga 840-8502, Japan

Abstract—Subsociality involving provisioning for offspring has been reported for one shield bug and three burrower bug species (Hemiptera: Pentatomoidea: Parastrachiidae and Cydnidae: Sehirinae). We present the first report of subsocial behaviour in the burrower bug *Adomerus variegatus* (Signoret), focusing on manifestations of maternal-care, specifically the production of trophic eggs, guarding of offspring, and progressive provisioning. In our study, each female produced an egg mass that included some trophic eggs. Prior to nymphal hatch, females remained in their nests and showed egg mass guarding behaviour. Mothers started provisioning behaviour a few hours after nymphal hatch. Each mother dragged a seed (larger than her body) with her proboscis to the nest as food for the nymphs. These findings suggest that *A. variegatus* shows maternal-care behaviours similar to those reported in some other pentatomoid species and that trophic egg production and nest provisioning have evolved as interrelated processes.

Résumé—On a signalé de la subsocialité comprenant de l'approvisionnement des rejetons chez une espèce de punaises à écusson et trois espèces de punaises fouisseuses (Heteroptera: Pentatomoidea: Parastrachiidae et Cydnidae: Sehirinae). Nous fournissons une première attestation d'un comportement subsocial chez la punaise fouisseuse *Adomerus variegatus* (Signoret), nous intéressant surtout aux manifestations des soins maternels, en particulier la production d'œufs trophiques, la surveillance des petits et l'approvisionnement progressif. Dans notre étude, les masses d'œufs de chaque femelle d'*A. variegatus* contiennent quelques œufs trophiques. Avant l'éclosion des larves, les femelles demeurent au nid et ont un comportement de garde de la masse d'œufs. Les mères commencent leur comportement d'approvisionnement quelques heures après l'éclosion des larves. Chaque mère traîne vers le nid une graine (plus grande que son propre corps) avec son rostre comme nourriture pour les larves. Ces observations indiquent qu'*A. variegatus* possède des comportements de soins

Received 5 May 2009. Accepted 11 August 2009.

[1]Corresponding author (e-mail: 09552203@edu.cc.saga-u.ac.jp).
doi: 10.4039/n09-045

 © 2010 Entomological Society of Canada

https://doi.org/10.4039/n09-045 Published online by Cambridge University Press

maternels semblables à ceux signalés chez d'autres espèces de pentatomoïdes et que les patrons de production d'œufs trophiques et d'approvisionnement au nid se sont développés comme des mécanismes associés.

[Traduit par la Rédaction]

It is surmised that subsocial behaviour, characterized by parental care for offspring, promoting offspring survival, growth, and development (Tallamy and Wood 1986), has evolved independently several times in the true bugs (Hemiptera) (Melber and Schmidt 1977; Tallamy and Schafer 1997). Females of some species of burrower bugs (Cydnidae: Sehirinae) and the closely related shield bugs (Parastrachiidae) display maternal-care behaviours, including egg guarding, production of trophic eggs, protection of nymphs against predators, and progressive provisioning (Filippi *et al.* 2001, 2008; Costa 2006). Interestingly, the patterns of these behaviour components vary somewhat among the closely related species investigated thus far. It is important to examine the range of variation in such behaviour patterns to gain an understanding of the evolution of subsociality, including provisioning, in the true bugs. In this study, therefore, we studied the reproductive behaviour of the sehirine burrower bug *Adomerus variegatus* (Signoret) in the field and laboratory, focusing on the production of trophic eggs, protection of offspring, and progressive provisioning. Prior to our study, no information existed on parental care in this species.

Adomerus variegatus inhabits deciduous forests in northern Japan and Russia (Lis 2006); in Japan, it feeds solely on the winged seeds of the Japanese elm, *Ulmus davidiana* Planch. var. *japonica* (Rehder) Nakai (Ulmaceae) (Sato 2003). Bugs were collected and observed in Shobugahama and Senjyugahama, near Tyuzenji Lake, Tochigi Prefecture, Japan (36°43′N, 139°29′E), on 5 May and 6–9 and 30 June 2008. Specimens were reared in an incubator in the laboratory at 18 °C and 16L:8D. Approximately 10 males and 10 females were mixed in each of three clear-plastic cups (13 cm × 6 cm) containing a moist Kimwipe. Five egg-guarding females were transferred with their eggs to individual clear-plastic cups (8 cm × 4 cm) and fed seeds of the host plant under the same conditions. Just before nymphal hatch, females and their egg masses were transferred from the cups to rectangular plastic containers (26 cm × 18 cm × 5 cm) large enough to allow provisioning behaviour to be observed, and kept at 23 °C under natural light. We prepared nests by covering one corner of the bottom of the container with a Kimwipe; the feeding site was at the opposite corner. We provided the bugs in each cup and each container with fresh host seeds and water daily. Three females with their egg masses were filmed with a video camera.

Eggs were laid in a spherical mass (Fig. 1*a*). Eyespots were observed after 12 days and synchronized nymphal hatch occurred 14 days after oviposition. To count the viable eggs and trophic eggs (nonviable eggs that served as food for the nymphs), we carefully separated the masses into small pieces. Some eggs in each egg mass never developed eyespots. We observed nymphs trying to insert their mouthpart stylets into the eggs that had no eyespots. These eggs shriveled and (or) disappeared within 24 h, so we concluded that they were trophic eggs prepared by the females before nymphal hatch (Crespi 1992).

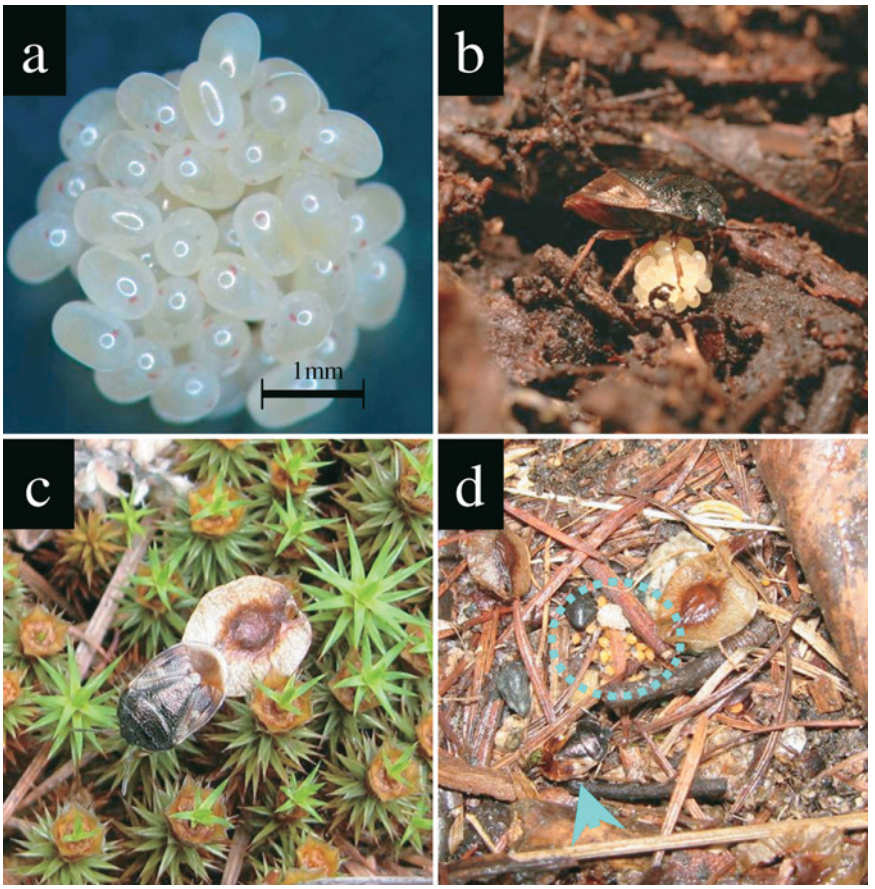
The numbers of total, viable, and trophic eggs in an egg mass were 77.0 ± 1.0 (mean ± SE), 73.3 ± 2.3, and 3.7 ± 2.0, respectively ($n = 3$). The mass of the egg mass remained constant during the egg-guarding period. This suggests that after initial oviposition, no further eggs are laid. We found no eggs in ovarioles dissected out of five mothers 13 days after oviposition. Thus, the pattern of trophic egg production by *A. variegatus* is similar to that by the shield bug *Parastrachia japonensis* (Scott) (Parastrachiidae) (Hironaka *et al.* 2005).

During the egg-guarding phase, each female remained in her nest with the eggs (Fig. 1*b*). At the time of observation, we never observed females feeding or found evidence (*e.g.*, endosperm denaturation) that they had fed

© 2010 Entomological Society of Canada

https://doi.org/10.4039/n09-045 Published online by Cambridge University Press

Fig. 1. Female, eggs, and nymphs of *Adomerus variegatus*: *a*, egg mass just before hatch; *b*, female guarding egg mass in the nest; *c*, female carrying *Ulmus* seed; *d*, female (arrowhead) with 1st-instar nymphs (dotted circle). Photographs *b*, *c*, and *d* were taken under natural conditions.



upon the seeds. Accordingly, we concluded that the females guarded the egg masses continuously for 14 days without feeding. During the egg-guarding period, each female held its egg mass under its abdomen with its legs and exhibited defensive guarding behaviour, using its back like a shield in response to stimulation with forceps. This behaviour was only seen during the egg-guarding period.

We observed the provisioning behaviour of three females in the laboratory and counted the daily changes in their provisioning frequency. Provisioning started immediately after nymphal hatch (Fig. 2), peaked in frequency at the 2nd nymphal moult, and declined in the middle of the 3rd stadium. The seeds were larger than the female's body; each female carried a seed by attaching its proboscis to the seed stalk, thus preventing the seed wings from interfering with leg movement (Fig. 1*c*). Under the rearing conditions employed, nymphs gradually became independent in the middle of the 4th stadium, when they were approximately 12 days old.

On 30 June we observed nesting and provisioning behaviour in the field. The nests were located 1–3 cm under leaf litter or moss (Fig. 1*d*). The numbers of nymphs and host seeds in seven nests were 38.3 $\pm$ 15.3 (mean $\pm$ SE) and 5.1 $\pm$ 2.3, respectively. The seed-carrying behaviour of 31 provisioning females observed in the field for 1 h between 1500 and 1600 was similar to that of the females in the laboratory.

© 2010 Entomological Society of Canada

https://doi.org/10.4039/n09-045 Published online by Cambridge University Press

Fig. 2. Daily changes in the frequency of provisioning of three nests by female *Adomerus variegatus* under laboratory conditions. The seeds carried into the nest were counted daily. Each line represents one female. The duration of each stadium is indicated.

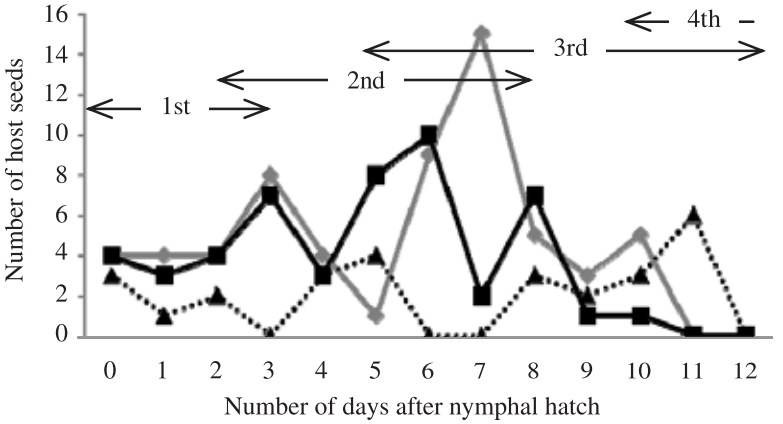


Table 1. Patterns of trophic egg production and provisioning in five species of pentatomoid Hemiptera.

	Sehirus cinctus[a] (Cydnidae)	*Adomerus triguttulus*[b] (Cydnidae)	*Canthophorus niveimarginatus*[c] (Cydnidae)	*Parastrachia japonensis*[d] (Parastrachiidae)	*Adomerus variegatus* (Cydnidae)
Timing of trophic egg production	Not known	Prehatch only	Pre- and post-hatch	Prehatch only	Prehatch only
Start of provisioning	1st stadium	1st stadium	2nd stadium	1st stadium	1st stadium
Clutch size (mean ± SE)	120–150[e]	69.2 ± 5.7	64.0 ± 3.1	130.5 ± 5.1	77.0 ± 1.0
No. of trophic eggs (mean ± SE)	—[f]	31.6 ± 1.7	6.2 ± 1.2 (prehatch); 26.1 ± 0.4 (posthatch)	41.7 ± 1.8	3.7 ± 2.0

Note: Standard errors were calculated by H.M.
[a]From Sites and McPherson (1982) and Kight (1997).
[b]From Nakahira (1994).
[c]From Filippi *et al.* (2008).
[d]From Tsukamoto and Tojo (1992); Hironaka *et al.* (2005).
[e]Mean and SE not available.
[f]Data not available.

In Hemiptera, a detailed quantitative assessment of the daily provisioning pattern in the laboratory has only been reported for *Canthophorus niveimarginatus* Scott (Cydnidae: Sehirinae): during the 1st stadium, nymphs feed solely on pre- and post-hatch trophic eggs, and maternal provisioning behaviour begins at the start of the 2nd stadium (Filippi *et al.* 2008). It is also known that *P. japonensis* (Tsukamoto and Tojo 1992) and the burrower bugs *Sehirus cinctus* (Palisot) (Sites and McPherson 1982; Kight 1997) and *Adomerus triguttulus* (Motchulsky) (Nakahira 1994) begin provisioning in the 1st instar. While *P. japonensis* (Hironaka *et al.* 2005) and *A. triguttulus* (Nakahira 1994) may produce a high number of prehatch trophic eggs (up to one-third of the egg mass), none of these species are known to provide posthatch trophic eggs (data for these species and *A. variegatus* are summarized in Table 1).

In our study, female *A. variegatus* produced a few prehatch, but no posthatch, trophic eggs and actively provisioned their nests during the

© 2010 Entomological Society of Canada

https://doi.org/10.4039/n09-045 Published online by Cambridge University Press

1st nymphal stadium. These findings, taken in the context of previous reports on related species (Table 1), suggest that patterns of trophic egg production and provisioning have evolved as interrelated processes. However, the ecological and physiological conditions under which provisioning behaviour evolved in pentatomoid bugs remain unclear. Comparison of maternal-care behaviours among these subsocial bugs will contribute significantly to our understanding of why progressive provisioning evolved in this group.

We thank S. Maehara for help with field observations, H. Nomiya for collecting the seeds used for provisioning, and S. Tojo for providing comments on our manuscript. This research was partially supported by a Grant-in-Aid for Young Scientists (B) (20770055) and a Grant-in-Aid for Scientific Research (18570025) from the Ministry of Education, Culture, Sports, Science and Technology of Japan.

Costa, J.T. 2006. The other insect societies. Harvard University Press, Cambridge, Massachusetts.

Crespi, B.J. 1992. Cannibalism and trophic eggs in subsocial and eusocial insects. *In* Cannibalism: ecology and evolution among diverse taxa. *Edited by* M.A. Elgar and B.J. Crespi. Oxford University Press, Oxford, United Kingdom, and New York. pp. 176–213.

Filippi, L., Hironaka, M., and Nomakuchi, S. 2001. A review of the ecological parameters and implications of subsociality in *Parastrachia japonensis* (Hemiptera: Cydnidae), a semelparous species that specializes on a poor resource. Population Ecology, **43**(1): 41–50. doi:10.1007/PL00012014.

Filippi, L., Baba, N., Inadomi, K., Yanagi, T., Hironaka, M., and Nomakuchi, S. 2008. Pre- and post-hatch trophic egg production in the subsocial burrower bug, *Canthophorus niveimarginatus* (Heteroptera: Cydnidae). Naturwissenschaften, **96**(2): 201–211. PMID:18846358 doi:10.1007/s00114-008-0463-z.

Hironaka, M., Nomakuchi, S., Iwakuma, S., and Filippi, L. 2005. Trophic egg production in a subsocial shield bug, *Parastrachia japonensis* Scott (Heteroptera: Parastrachiidae), and its functional value. Ethology, **111**(12): 1089–1102. doi:10.1111/j.1439-0310.2005.01112.x.

Kight, S.L. 1997. Factors influencing maternal behaviour in a burrower bug, *Sehirus cinctus* (Heteroptera: Cydnidae). Animal Behaviour, **53**(1): 105–112. doi:10.1006/anbe.1996.0282.

Lis, J.A. 2006. Family Cydnidae. *In* Catalogue of the Heteroptera of the Palaearctic Region. Vol. 5. *Edited by* B. Aukema and C. Rieger. The Netherlands Entomological Society, Amsterdam. pp. 118–147.

Melber, A., and Schmidt, G.H. 1977. Sozialphänomene bei Heteropteren. Zoologica (Stuttgart), **127**: 19–53.

Nakahira, T. 1994. Production of trophic eggs in the subsocial burrower bug, *Admerus(sic) triguttulus.* Naturwissenschaften, **81**: 413–414.

Sato, K. 2003. Distribution of Heteroptera in Tochigi Prefecture (6). Insekuto, **54**: 77–78. [In Japanese.]

Sites, R.W., and McPherson, J.E. 1982. Life history and laboratory rearing of *Sehirus cinctus cinctus* (Hemiptera: Cydnidae), with descriptions of immature stages. Annals of the Entomological Society of America, **75**: 210–215.

Tallamy, D.W., and Schaefer, C. 1997. Maternal care in the Hemiptera: ancestry, alternatives, and current adaptive value. *In* The evolution of social behavior in insects and arachnids. *Edited by* J. Choe and B. Crespi. Cambridge University Press, London, United Kingdom. pp. 94–115.

Tallamy, D.W., and Wood, T.K. 1986. Convergence patterns in subsocial insects. Annual Review of Entomology, **31**(1): 369–390. doi:10.1146/annurev.en.31.010186.002101.

Tsukamoto, L., and Tojo, S. 1992. A report of progressive provisioning in a stink bug, *Parastrachia japonensis* (Hemiptera: Cydnidae). Journal of Ethology, **10**(1): 21–29. doi:10.1007/BF02350183.

© 2010 Entomological Society of Canada

https://doi.org/10.4039/n09-045 Published online by Cambridge University Press