Trophic-egg production in a subsocial bug: adaptive plasticity in response to resource conditions

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Kudo, S. and Nakahira, T. 2005. Trophic-egg production in a subsocial bug: adaptive plasticity in response to resource conditions. – Oikos 111: 459–464.

Adomerus triguttulus (Heteroptera: Cydnidae) females provision host *Lamium* spp. seeds to their nymphs. Females also produce trophic eggs, which are inviable and usually function as a food supply for hatched nymphs. Here we report experimental evidence of the potentially adaptive maternal effects of this unusual resource investment. To investigate the effects of food-resource environments on trophic-egg production, we reared females under different resource conditions prior to oviposition and then compared the subsequent allocations of trophic eggs. Females that had been supplied with less-developed seeds produced fewer viable eggs than those supplied with well-developed seeds. However, there was no difference in the number of trophic eggs produced between the two treatments, and thus the trophic-egg ratio, i.e. the number of trophic eggs per viable egg, was higher in females supplied with less-developed seeds. Trophic-egg feeding by hatched nymphs enhances their growth or survival, and a higher trophic-egg ratio would be adaptive particularly under limited resource conditions. In *A. triguttulus*, adults and offspring depend on the same food resource, i.e. host seeds, and the resource conditions experienced by females prior to oviposition should be well correlated with those experienced later by the offspring. This may enable females to adjust the trophic-egg ratio in response to varying resource environments prior to oviposition.

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Maternal effects, the components of an offspring phenotype that are determined by the maternal environment, can have remarkable consequences for the life history of the progeny (Fox and Mousseau 1998). The effects are common among animal and plant taxa, and have attracted enormous interest among ecologists and evolutionary biologists. The maternal effects are expressed through parental care, oviposition behaviour, and most frequently, provisioning to eggs (Bernardo 1996, Fox and Mousseau 1998).

In temporally and spatially heterogeneous environments, egg-size variance might be favoured by natural selection (Kaplan and Cooper 1984, Philippi and Seger 1989). On the other hand, egg-size plasticity would be

favoured where the female that experiences a predictive environmental cue variably allocates resources to her offspring appropriate for the conditions predicted by the cue (Mousseau and Dingle 1991, Bernardo 1996, Fox and Mousseau 1998). Some arthropod taxa exhibit plasticity in egg size, which is sometimes associated with environmental factors (Burns 1995, Kawecki 1995, Braby and Jones 1995, McKee and Ebert 1996, Fox et al. 1997, Rotem et al. 2003). Maternal diet is one such external factor affecting egg size. It is generally expected that as food stress increases, consequently inducing lower offspring survival, females should invest more in each offspring (reviewed by Clutton-Brock 1991, Roff 2002). However, many results inconsistent with this

prediction have been reported in previous studies using arthropods (reviewed by Fox and Czesak 2000). Thus the adaptiveness of maternal effects, i.e. egg-size plasticity in response to maternal environments, remains unclear in arthropods.

Egg size generally determines the upper limit to the amount of nutritional resources required to support embryonic development. However, females do not only provide material resources to their offspring through developing oocytes before ovulation; in some arthropod taxa, matrotrophy, i.e. nutritional transfer to offspring after ovulation within the female body, has also been reported (Stay and Coop 1973, Bontems 1988). Trophic eggs, inviable eggs that usually function as a food supply for hatched siblings, also can be regarded as extended maternal investment (Alexander 1974, Polis 1984), although there is some controversy concerning its evolutionary origin (Crespi 1992, Mock and Parker 1997, Kudo and Nakahira 2004). There are many examples in which hatchlings eat unfertilized or undeveloped eggs and/or viable eggs in the same clutch (Osawa 1989, Dickinson 1992; reviewed by Elgar and Crespi 1992, Mock and Parker 1997). With the exception of eusocial hymenopteran insects, however, trophic eggs which are functionally and morphologically differentiated, are known in only a few arthropod taxa (West and Alexander 1963, Henry 1972, Kim and Roland 2000; reviewed by Crespi 1992).

Adomerus triguttulus (Motschulsky) (Heteroptera: Cydnidae) is a subsocial burrower bug. *A. triguttulus* females show a complex pattern of parental care, including trophic-egg production during egg care and progressive provisioning of host seeds to hatched nymphs (Nakahira 1992, 1994). Kudo and Nakahira (2004) have experimentally demonstrated the nutritional advantage of trophic-egg feeding by hatched nymphs.

In this paper, we investigated plasticity in trophic-egg production in response to varying food resources in *A. triguttulus*. To clarify the effects of the resource environments experienced by females on trophic-egg production, we reared females prior to oviposition in two experimental groups under different resource conditions and compared trophic-egg allocation between the groups.

Material and methods

Reproductive history of *Adomerus triguttulus*

Overwintered *A. triguttulus* females breed from late May to June in Sapporo, northern Japan (Nakahira 1992). The females feed upon developing seeds of the host *Lamium* spp. Gravid females move from the plant to the ground and lay eggs in shallow chambers under the leaf litter; they form spherical egg masses almost within a day and then attend the egg-mass (Nakahira 1992,

1994). During egg care, females continue to produce trophic eggs and add them to the egg mass (Nakahira 1994). Trophic eggs in *A. triguttulus* are morphologically specialized; they are usually smaller in volume and have a different chorion structure to that of viable eggs, lacking micropyles (S. Kudo, T. Nakahira and Y. Saito, unpubl.). The body size of females affects their reproductive output: larger females produce more viable eggs with relatively fewer trophic eggs (Kudo and Nakahira 2004). Trophic-egg feeding by hatched nymphs enhances their growth and survival (Kudo and Nakahira 2004). After hatching, the females show progressive provisioning; they temporarily leave their broods and transport seeds to feed them. Maternal care usually ends within the second instar (Nakahira 1992).

Rearing

Overwintered females were collected as soon as they appeared on the mint *Lamium purpureum* in the Hokkaido University campus. They were individually confined in plastic petri dishes (9 cm diameter, 1 cm height) with moderately moist filter paper. There may have been variation in body condition, i.e. fat-body development and/or ovarian development, among females at the time of collection. To reduce the effects of possible variation in female condition at the time of field collection on the subsequent experiments, the females were kept without food (but with water) for ten days under 16L:8D photoperiod, 10°C conditions. This starvation treatment probably causes the degeneration of developing young oocytes in the females (Bell and Bohm 1975). They were then transferred to 20°C and males were added to allow the female to mate. Paper shelters were placed in each petri-dish for oviposition sites. The males were removed from the petri dishes after oviposition commenced.

Resource manipulation experiments

To investigate the effects of the resource conditions experienced by females before oviposition (during the oogenesis of viable eggs), we randomly divided females which had received the starvation treatment into two experimental groups: the rich-resource group (R) in which females were supplied with well-developed host seeds, and the poor-resource group (P) in which females were supplied with less-developed seeds. We provided several pieces of *L. purpureum* inflorescences attaching seeds of one of the two categories to each female. Females sometimes feed on host seeds during egg care (Nakahira 1992). Variation in the degree of seed-feeding among females during egg care (and the oogenesis of trophic eggs) might confound the results of the experiments. Therefore, we removed seeds from the petri-dishes

in both experimental groups just after the start of oviposition, and thus no seeds were available to females during the care of eggs and trophic-egg production. Even where there are no available seeds after the start of oviposition, females produce trophic eggs (Nakahira 1992). We weighed several females that had been randomly chosen from each of the two experimental groups to monitor their body conditions until the start of oviposition. The resource manipulation caused remarkable differences in body conditions just before oviposition between females in the two groups.

We compared the allocation of trophic eggs and viable eggs between the clutches of the poor-resource and rich-resource groups. Viable eggs usually hatch on the eleventh day after the start of oviposition under the rearing conditions used in this experiment (Nakahira 1992, 1994). On the tenth day after the start of oviposition, just before hatching, we carefully separated the clutches into small clumps consisting of a few eggs using a fine brush and forceps and counted the numbers of viable and trophic eggs contained in each clutch. Viable eggs are easily distinguished from trophic eggs by possessing developed embryos with pigmented eyespots at the time close to hatching.

Results

There was no significant difference in female body size (prothorax width) between the rich-resource and the poor-resource groups (mean $\pm$ SD mm; rich-resource, 2.66 ± 0.12; poor-resource, 2.70 ± 0.13; $t_{60} = -1.20$, P = 0.23). The experimental manipulation of food conditions caused a decrease in female body weight, which reflects the total amount of retained viable eggs and reserves for trophic-egg production, just before the start of viable-egg deposition. Females in the rich-resource group were significantly heavier than those in the poor-resource group (ANCOVA with female body size as a covariate: interaction, $F_{1,34} = 0.26$, P = 0.61 and treatment effect in the reduced model, $F_{1,35} = 87.73$, p < 0.001; Fig. 1).

Female body size positively affected the number of viable eggs in the poor-resource group (r = 0.464, P = 0.025), but not in the rich-resource group (r = 0.243, P = 0.14). There were no significant relationships between female body size and the number of trophic eggs (poor-resource, r = 0.154, P = 0.49; rich-resource, r = 0.226, P = 0.17). No significant phenotypic trade-offs were detected between numbers of viable and trophic eggs even when controlling the body-size effects (poor-resource, partial r = 0.138, P = 0.53; rich-resource, partial r = −0.311, P = 0.05).

Females in the poor-resource group laid significantly fewer viable eggs than those in the rich-resource group (ANCOVA with the female body size as a covariate: interaction, $F_{1,58} = 0.17$, P = 0.68 and treatment effect in
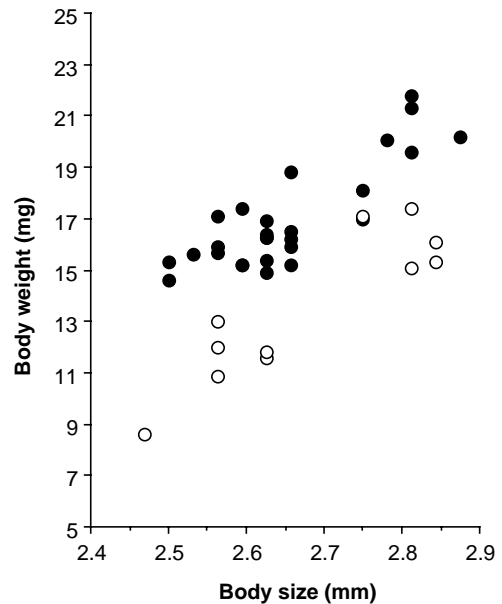

Fig. 1. Effect of different resource conditions that females experienced on their body weight at oviposition. The body weight one day before the start of oviposition is shown for females in the following groups; the rich-resource group in which females were reared with well-developed seeds until the start of oviposition (closed circles, n = 27) and the poor-resource group in which females were reared with less-developed seeds (open circles, n = 11).

the reduced model, $F_{1,59} = 39.50$, P < 0.001; Fig. 2a). However, there was no significant difference in the number of trophic eggs produced by females between the two groups ($t_{65} = 0.57$, P = 0.57; Fig. 2a). Consequently, the trophic-egg ratio, the number of trophic eggs per viable egg, was higher in females that had been maintained in poor resource conditions (ANCOVA with the female body size as a covariate: interaction, $F_{1,58} = 3.06$, P = 0.09 and treatment effect in the reduced model, $F_{1,59} = 6.37$, P = 0.014; Fig. 2b).

Discussion

The resource manipulation experiments demonstrated that *A. triguttulus* females enhanced relative trophic-egg investment when they had experienced poor food-resource conditions. It is most likely that the decreased number of viable eggs was caused directly by poor nutrition available during oogenesis (Wheeler 1996). However, the females that had experienced poor food conditions did not inhibit trophic-egg production despite no available food during most of their oogenesis. Females do not complete trophic-egg maturation in their ovaries at the deposition of viable eggs, and they continue to develop oocytes and to lay trophic eggs during maternal care (Nakahira 1994, S. Kudo, T. Nakahira and Y. Saito, unpubl.). Thus, the observed
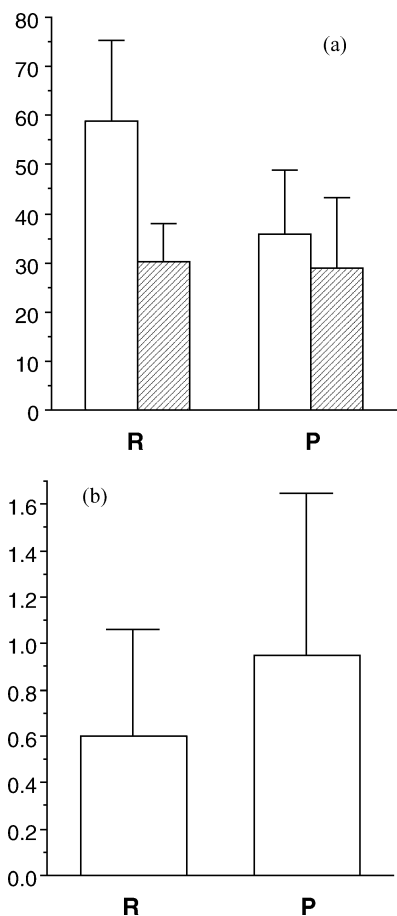
Fig. 2. Effect of different resource conditions that females experienced on subsequent trophic-egg investment. (a) Numbers of viable eggs (open columns) and trophic eggs (shaded columns). (b) Trophic-egg ratio, the number of trophic eggs per viable egg. The parameters were measured at the tenth day after the start of oviposition (just before hatching) in the following groups; R: the rich-resource group in which females were reared with well-developed seeds until the start of oviposition (n = 39) and P: the poor-resource group in which females were reared with less-developed seeds (n = 23). In the both groups, the seeds were removed just after the start of oviposition.

high trophic-egg ratio is apparently the outcome of active oogenesis of trophic eggs during maternal care. Trophic-egg feeding greatly enhances offspring survival under food shortages, and even when food is available, increasing the trophic-egg ratio promotes nymphal growth (Kudo and Nakahira 2004). It is most likely that optimal trophic-egg investment is higher where the risks of food shortages for offspring are higher. There are remarkable differences in seed productivity between *Lamium* spp. Reproductive traits of females that breed on *L. album* are different from those on *L. purpureum*; smaller brood size of the former seems to correspond with lower resource availability for *A. triguttulus* offspring (S. Kudo and T. Nakahira,

unpubl.). Seed production (its quality and density on the ground) greatly varies in time and space within a single *Lamium* species as well as among different species (S. Kudo and T. Nakahira, unpubl.). Such resource environment heterogeneity would be an essential selective factor for the evolution of subsocial behaviour including trophic-egg production and its adjustment in *A. triguttulus* (Nakahira 1994, Kudo and Nakahira 2004). It has been suggested that resource availability affects sibling oophagy in a few insects (Osawa 1989). However, there has been no study revealing maternal adjustment of relative trophic-egg production in response to varying resource environments. This study is, to the best of our knowledge, the first to indicate the potentially adaptive plasticity of trophic-egg production in non-eusocial arthropods.

It has been theoretically expected that, as food stress increases and induces low offspring survival, females should invest more resources in each offspring (Parker and Begon 1986, Sibly and Calow 1986, reviewed by Clutton-Brock 1991, Roff 2002). Some studies on offspring-size plasticity in vertebrates suggest such adaptive maternal effects (Reznick and Yang 1993, Reznick et al. 1996). In arthropods, this tendency (at least, within a certain range of food stress) has been supported in studies using crustaceans (Brody and Lawlor 1984, Perrin 1989, Glazier 1992, Gliwicz and Guisande 1992, Ebert 1994, Burns 1995, McKee and Ebert 1996, Boersma 1997). However, it is often not the case in other taxa; food stress on females does not affect egg size (Hill and Pierce 1989, Hard and Bradshaw 1993, Ernsting and Isaaks 1997), or rather, it induces females to produce smaller eggs (Kessler 1971, Harvey 1983, Murphy et al. 1983, Steinwascher 1985, Fox 1993, Braby and Jones 1995, Ekbom and Popov 2004), which is suggestive of a physiological constraint rather than an adaptation. Such inconsistency is possibly due to differences in the nutritional ecologies of female parents and offspring among the studied taxa. When food resource conditions for females are well correlated with those of their offspring, previously experienced resource-conditions could be employed as reliable cues for females to adjust maternal investment (Bernardo 1996). By contrast, when there is no correlation between food resource conditions for the parent female and for her offspring, such cues are not available. The timing of, and the period required for the completion of oogenesis can cause a large time lag between the acquisition of environmental information by females and the accomplishment of optimally-sized eggs and oviposition. This time lag may make the maternal diet less reliable as a cue for future resource conditions for offspring. A variety of life history characters, such as voltinism, generation time and migration, in combination with the persistency or seasonality of resource quality and/or quantity can be associated with the reliability of the maternal diet as a

predictable cue. In *A. triguttulus*, overwintered females feed on the developing seeds of host plants and soon (within several weeks) breed on the ground within or around host-plant patches (Nakahira 1992). It is most likely that the quality and quantity of fallen seeds available for offspring are, even in fine-spatial scales, correlated with those experienced by the female. This may enable females to adaptively adjust trophic-egg ratio in response to varying resource environments before oviposition.

In insects, there are only a few examples in which females respond to their oviposition environments by adjusting egg size (Fox et al. 1997, Fox and Mousseau 1998). As well as ecological factors, physiological mechanisms of oogenesis may also constrain the immediate adjustment of maternal investment. In arthropods, nutritional investment for individual eggs (and thus for embryos) can not usually be altered after ovulation (completion of oocyte maturation). However, even after the maturation and the deposition of viable eggs, females could change their nutritional investment through trophic eggs. Despite inevitable resource loss through the digestive processes of trophic eggs, trophic-egg production and consumption by hatchlings would be a way of providing flexible resource economy under variable resource environments.

Increased parental effort, including trophic-egg production, may incur reproductive and/or survival costs upon females (Clutton-Brock 1991, Stearns 1992, Roff 2002). In particular, trophic-egg production could potentially reduce the current brood size, although no phenotypic tradeoff between the numbers of viable and trophic eggs have been detected in *A. triguttulus* (Kudo and Nakahira 2004). *A. triguttulus* females have another option of brood provisioning; as in other subsocial cydnid bugs (Filippi-Tsukamoto et al. 1995, Kight 1997, Filippi et al. 2000, Agrawal et al. 2001), females transport host seeds to their hatched nymphs (Nakahira 1992). Poor resource conditions might promote higher maternal efforts in seed-provisioning behaviour, instead of trophic-egg production. In order to search for and collect a sufficient amount of seeds under such poor resource conditions, however, females may have to leave their broods frequently and for a long period. Increased foraging time by females probably increases predation risk for nymphs in the nest. *Lamium* spp. are myrmecochorous plants; they attract foraging ants using a nutritional material, elaiosome, which is attached to seeds, and their seed dispersal depends on these ants (Beattie 1985). The density of foraging ants is always high on and around plants and this can lead to high predation pressure against herbivores, in particular, seed-feeders foraging on the ground. Experimental removal of *A. triguttulus* brooding females in the field has revealed that predation pressure by arthropods against offspring is potentially severe and the brooding females provide effective defense (Nakahira 1992). It is possible that predation by arthropods, especially by ants, would inhibit increased maternal seed-provisioning efforts and instead favour increased trophic-egg investment under poor resource conditions.

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Subject Editor: Stig Larsson