Effects of trophic-eggs on offspring performance and rivalry in a sub-social bug

Shin-ichi Kudo and Taichi Nakahira

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Trophic eggs, which are inviable and usually function as a food supply for offspring, have been regarded as extended parental investment or the outcome of parent–offspring conflict in sibling oophagy. *Adomerus triguttulus* (Heteroptera: Cydnidae) is a sub-social bug showing a complex pattern of maternal care, including progressive provisioning of host seeds and trophic-egg production. To investigate the functions of trophic eggs, we removed trophic eggs from clutches under different resource conditions. The longevity of nymphs was greatly extended by feeding upon trophic eggs when seeds were excluded. When seeds were provided, trophic-egg feeding by nymphs enhanced their development, but there were no significant effects on brood survival. Some viable eggs were also fed upon by sibling nymphs. However, there was no difference in the proportion of viable eggs consumed between clutches with and without trophic eggs. Females lay viable eggs within the first oviposition day. The synchronous hatching resulting from this oviposition mode seems to prevent sib-cannibalism. The body size of females affected their relative investment in trophic eggs; larger females produced more viable eggs with relatively fewer trophic eggs. The functions and adaptive allocation of trophic eggs are discussed in light of the two hypotheses mentioned above.

S. Kudo, Dept of Biology, Naruto Univ. of Education, JP-772-8502 Naruto, Japan (skudo@naruto-u.ac.jp). – T. Nakahiar, Systematic Entomology, Faculty of Agriculture, Hokkaido Univ., JP-060-8589 Sapporo, Japan.

Oophagy is known in a variety of invertebrates (reviewed by Elgar and Crespi 1992) and is often conducted by siblings within clutches (Osawa 1989). Such sibling oophagy is usually associated with hatching asynchrony and unsuccessful hatching including infertile eggs (Kawai 1978, Baur and Baur 1986), but morphological and/or functional differentiation of victim eggs has also been reported (Henry 1972, Kim and Roland 2000).

Trophic eggs are defined as eggs or egg-like structures that are inviable and usually function as a food supply for offspring. They have been regarded as extended parental investment (icebox hypothesis: Alexander 1974, Polis 1984). By contrast, some authors have discussed the evolution of trophic eggs in the context of parent–offspring conflict (Crespi 1992). Where there is sibling cannibalism, the optimal cannibalism rate is higher for offspring than for the mother, because offspring are more closely related to themselves than to their siblings or their mother (Trivers 1974). If an offspring consumes siblings, it would be in the mother's interests to provide less expensive alternatives for consumption. The mother may make some eggs inviable and less costly, and thus trophic-egg production would be favoured (Crespi 1992). Costs and benefits in both parents and offspring will affect the adaptive significance of trophic-egg production and consumption. Several factors, within-brood

relatedness, maternal phenotype and environmental conditions, particularly resource availability, would affect such a cost–benefit balance in the optimal allocation of trophic eggs from the parental and the offspring point of view.

Trophic eggs are well known in several groups of eusocial Hymenoptera (reviewed by Sakagami 1982, Hölldobler and Wilson 1990, Crespi 1992, Kukuk 1992). Caste differentiation among colony members has been established in such eusocial Hymenoptera, and thus trophic eggs could have different social or ecological significances and there could be complicated conflicts among the colony members (Crespi 1992). It would be difficult to clarify the origin and the evolution of trophic eggs in such systems. By contrast, non-eusocial taxa may provide clues to the controversial issues. In particular, sub-social species with trophic-egg production will be an interesting system for analyzing the allocation of parental investment in different parental options, and conflicts between female parents and offspring over the investment. However, there have also been a few non-eusocial insects in which trophic-egg production is known (Henry 1972). Both trophic-egg production and parental care have been observed only in a short-tailed cricket, *Anurogryllus muticus* (West and Alexander 1963), but no quantitative studies have been made.

Adomerus triguttulus (Motschulsky; Heteroptera: Cydnidae) is a sub-social true bug showing a complex pattern of maternal care, including progressive provisioning of host seeds to nymphs. Nakahira (1994) discovered trophic-egg production in this species.

In this paper, we investigate the functions of trophic eggs in *A. triguttulus* by the experimental removal of trophic eggs under different food-resource conditions; we compare performances, including the incidence of viable-egg cannibalism, of nymphs with trophic eggs and those without trophic eggs. Furthermore, we analyze the allocation of viable eggs and trophic eggs according to maternal phenotype. This is the first quantitative study on the adaptive significance of trophic eggs in sub-social insects.

Material and methods

Reproductive history of *Adomerus triguttulus*

Overwintered *A. triguttulus* females breed from May to June in Sapporo, the northern part of Japan (Nakahira 1992). The females feed upon developing seeds on the host *Lamium* spp. and move from the plant to the ground for oviposition. In shallow chambers under the leaf litter, females deposit eggs and form the spherical egg-mass almost within a day (Nakahira 1992, 1994) and then attend the egg-mass. Females with egg-masses show an aggressive display when disturbed. After a severe disturbance, the females often carry their egg-masses away from the disturbance.

During the egg-care the females sometimes temporarily leave eggs to feed upon seeds. They continue to produce trophic eggs and add them onto the egg-mass until hatching (Nakahira 1994). These trophic eggs are not simply the results of unsuccessful fertilization; they have a different chorion structure to that of viable eggs (Kudo et al., unpubl.). Even where there are no available seeds during maternal care, females produce trophic eggs (Nakahira 1992, unpubl.). After hatching, the females show progressive provisioning; they temporarily leave broods and transport seeds to feed them. Maternal care usually ends within the second instar (Nakahira 1992). In the later instar, nymphs forage for seeds maintaining small groups or individually on the ground. Cannibalism among the later-instar nymphs is often observed in the field (Nakahira, unpubl.).

Sampling and rearing

Gravid females with swollen abdomens were collected on the mint *Lamium album* in the Hokkaido University campus. They were individually confined in plastic petri dishes (9×1 cm) with moderately moist filter paper and host seeds, and were kept at 20°C with a 16: 8 h light: dark regime. A paper shelter was placed in each petri dish for oviposition sites. The females started oviposition within a few days after collection. Viable eggs usually hatch on the eleventh day after the start of oviposition (Nakahira 1992, 1994). Viable eggs are easily distinguished from trophic eggs by possessing developed embryos with pigmented eyespots at the time close to hatching.

Trophic-egg removal experiments under seed-provided conditions

Clutches were divided into the following two experimental groups. The trophic-egg removed group (n = 22): females were removed from clutches on the day subsequent to the start of oviposition, and thus no trophic eggs were contained in clutches. On the day after hatching, six host seeds were placed around an aggregation of first-instar nymphs in each petri dish. The control group (n = 21): females were kept intact after oviposition occurred. Host seeds were removed from the petri dish before hatching. On the day after hatching, the female was removed and six seeds were provided in each petri dish. In both experimental groups, ten new seeds were provided two days later and the original six seeds were removed at that time. The total number of seeds supplied to offspring during the experiments was within a range of that found with the brood under field conditions (Nakahira, unpubl.).

Prothorax width of the females was measured under a stereoscopic microscope using an ocular micrometer and was used for female body size in the subsequent analyses. There was no significant difference in the female body size between the two groups (mean $\pm$ SD, trophic-egg removed, 2.68 ± 0.15 mm; control, 2.72 ± 0.13 mm, $t_{41} = 0.93$, $P = 0.36$). On the sixth day after hatching, the number of survivors, all of which were in the second instar, was counted and their total weight was measured for each brood in both experimental groups to the nearest 0.01 mg using an electronic balance (Sartorius AG).

Allocation and consumption of trophic eggs

Using the control group in the above experiments, we investigated the allocation of viable and trophic eggs in clutches by females and their consumption by hatched nymphs. Three to five days after the start of oviposition, we removed the clutches temporarily from petri-dishes and carefully separated them into small pieces consisting of a few eggs using a fine brush and forceps. This separation of eggs allowed us to count the number of viable and trophic eggs later. Soon after counting, the eggs were gathered into a single cluster on the filter paper. These manipulations did not cause females to desert their offspring. Clutches in the trophic-egg removed group were also manipulated in the same manner. On the tenth day after the start of oviposition, just before hatching, we counted the numbers of viable eggs and trophic eggs contained in each clutch.

On the second day after hatching we counted the numbers of trophic eggs and viable eggs both of which had been sucked and crushed by hatchlings. The cannibalized (trophic and viable) eggs had no visible cleavage and contained remains, thus they could be distinguished from egg-shells left after hatching, which had a large cleavage and contained no remains. Furthermore, the cannibalized trophic eggs could be distinguished from the cannibalized viable eggs, because only the latter contained remains of pigmented embryos within.

Trophic-egg removal experiments under seed-excluded conditions

Clutches were divided into two experimental groups: the trophic-egg removed group ($n = 8$) in which females were removed from clutches on the day subsequent to the start of (viable egg) oviposition, and thus no trophic eggs were contained in clutches, and the control group ($n = 9$) in which females attended their clutches and laid trophic eggs on them. On the day after hatching, the females were removed from their broods. No host seeds were provided after the start of oviposition in both groups.

The number of surviving nymphs and their developmental stages were recorded daily.

Results

Allocation of trophic eggs under seed-provided conditions

Female phenotype affected allocation patterns of trophic eggs and viable eggs. Larger females produced more viable eggs ($r = 0.738$, $n = 21$, $P < 0.001$; Fig. 1a). However, there was no significant correlation between female body size and the number of trophic eggs ($r = 0.266$, $n = 21$, $P = 0.25$; Fig. 1a). There was no significant correlation between the number of viable eggs and that of trophic eggs ($r = 0.269$, $n = 21$, $P = 0.24$).
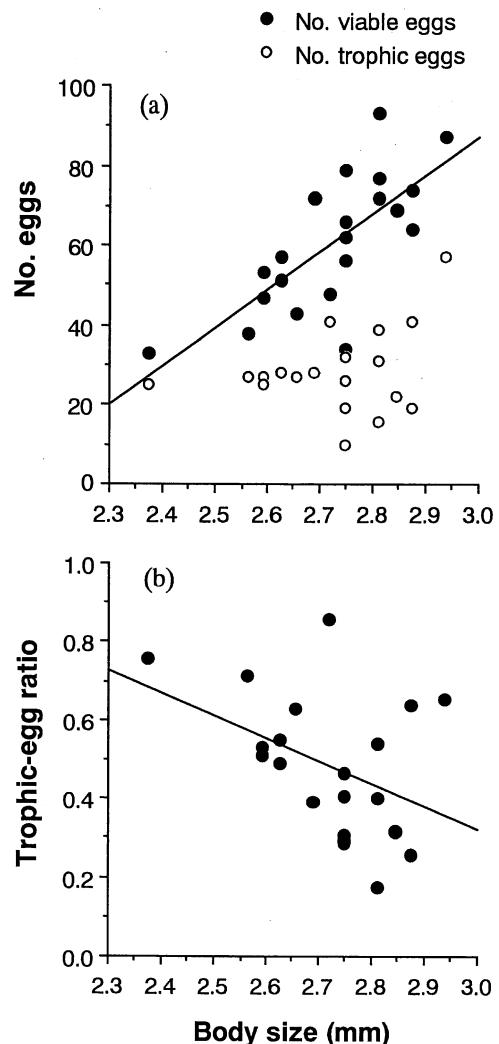

Fig. 1. The relationship between female body-size (prothorax width) and (a) the number of viable eggs and trophic eggs, and (b) the trophic egg ratio (number of trophic eggs per viable egg).

Even when the effects of female body size were controlled using residuals of the numbers of viable eggs and trophic eggs regressed against the female body size, no significant phenotypic trade-off was detected between them (partial $r = 0.112$, $n = 21$, $P = 0.48$).

There was large variation in the trophic-egg ratio, i.e. the number of trophic eggs per viable egg, among clutches. The trophic-egg ratio was negatively correlated with the number of viable eggs in clutches ($r = -0.495$, $n = 21$, $P = 0.022$). There was also a negative correlation (although it was statistically marginal) between the trophic-egg ratio and female body size ($r = -0.420$, $n = 21$, $P = 0.057$; Fig. 1b). This indicates that larger females produced clutches containing more viable eggs with relatively fewer trophic eggs.

Trophic-egg removal experiments under seed-provided conditions

There was no significant difference in the number of viable eggs (mean $\pm$ SD, trophic-egg removed, 55.55 ± 19.68; control, 60.71 ± 16.92, $t_{41} = 0.92$, $P = 0.36$) and the number of hatched nymphs (trophic-egg removed, 44.36 ± 16.33; control, 48.48 ± 17.36, $t_{41} = 0.80$, $P = 0.43$) between the trophic-egg removed and the control groups. Under conditions with seeds, the removal of trophic eggs did not affect offspring survival at the sixth day after hatching (data were arcsin square-root transformed before analysis, $t_{75} = 1.05$, $P = 0.30$; Fig. 2a). There was no significant relationship between the trophic-egg ratio and offspring survival in the control group ($r = 0.240$, $n = 21$, $P = 0.30$). However, trophic-egg feeding by nymphs enhanced their growth. Brood weight increased with the increasing number of viable eggs ($r = 0.783$, $n = 22$, $P < 0.001$ in the trophic-egg removed group; but the relationship was not significant in the control group, $r = 0.295$, $n = 21$, $P = 0.20$). Broods were heavier in the control group than in the trophic-egg removed group (ANCOVA with the number of viable eggs as a covariate: interaction, $F_{1,73} = 1.52$, $P = 0.22$ and group effect in the reduced model, $F_{1,74} = 12.22$, $P < 0.001$; Fig. 2b). On the other hand, nymphal weight (brood weight / number of nymphs) decreased in clutches with more viable eggs ($r = -0.528$, $n = 21$, $P = 0.013$ in the control group; but the relationship was not significant in the trophic-egg removed group, $r = -0.188$, $n = 22$, $P = 0.41$). Nymphs in the control group were significantly heavier than those in the trophic-egg removed group (ANCOVA with the number of viable eggs as a covariate, interaction, $F_{1,73} = 2.99$, $P = 0.09$ and group effect in the reduced model, $F_{1,74} = 11.62$, $P = 0.001$; Fig. 2c). In the control broods, the nymph weight increased with trophic-egg ratio ($r = 0.632$, $n = 21$, $P = 0.002$).

Almost all trophic eggs were fed upon by hatched nymphs within one day; only a few remained intact (in four out of 21 broods) at the time of examination (mean $\pm$ SD $= 1.00 \pm 2.95$ eggs). Moreover, some viable eggs were also eaten by siblings. No significant correlations were detected between the number of viable eggs and the proportion of those cannibalized in clutches of the control (the latter data were arcsin square-root transformed before analysis, $r = 0.116$, $n = 21$, $P = 0.62$) and the trophic-egg removed groups ($r = -0.357$, $n = 22$, $P = 0.10$). There was no significant difference in the proportion of viable eggs cannibalized between both groups (Mann–Whitney U-test, Z corrected for ties $= -0.832$, $P = 0.41$; Fig. 2d).

Trophic-egg removal experiments under seed-excluded conditions

There was no significant difference in the number of hatched nymphs between the trophic-egg removed and the control groups (mean $\pm$ SD, trophic-egg removed, 64.89 ± 25.25; control, 48.75 ± 10.32, $t_{15} = 1.68$, $P = 0.11$). The longevity of nymphs was greatly extended by feeding upon trophic eggs when deprived of seeds (data based on the individuals which lived longest in each brood, trophic-egg removed, mean $\pm$ SD $= 3.88 \pm 0.84$ days; control, 6.78 ± 0.97 days, $t_{15} = 6.56$, $P < 0.001$; Fig. 3). Nymphs never moulted into second instar in broods without trophic eggs, whereas some nymphs (mean $\pm$ SD $= 17.6 \pm 0.21\%$) successfully did so in 8 out of the 9 control broods.

Discussion

Sub-social insects with sib-cannibalism and trophic-egg production would be interesting systems for evaluating adaptive allocation of parental investment under parent–offspring conflict. Nevertheless, there have been no studies quantifying the cost and benefit of trophic-egg production and consumption in the sub-social insects. In *A. triguttulus*, trophic eggs apparently function as a food supply for hatched nymphs, and their nutritional benefit is high as reported in different taxa with sibling oophagy (Baur 1990, Osawa 1992, 2002, Kim and Roland 2000; reviewed by Elgar and Crespi 1992, Mock and Parker 1997). The trophic-egg removal experiments demonstrated that the growth of nymphs was enhanced by trophic-egg feeding when host seeds were provided. When deprived of seeds, the hatched nymphs which had fed on trophic eggs lived longer and some moulted into the second instar, although their moultings were apparently delayed as compared with those of nymphs feeding on seeds (Kudo and Nakahira, unpubl.).
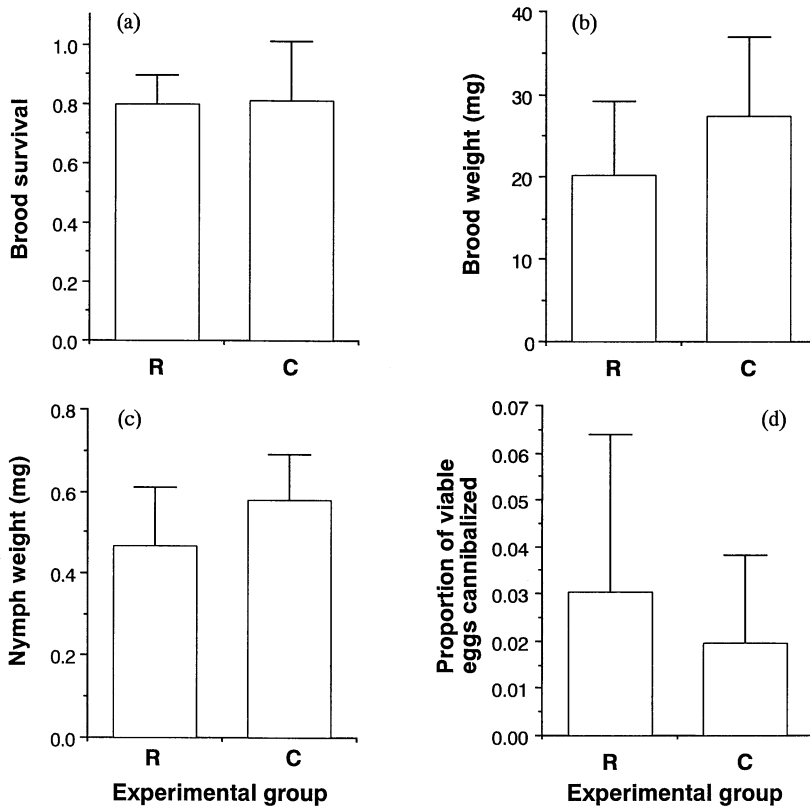
Fig. 2. The results of trophic-egg removal experiments under seed-provided conditions. (a) Brood survival. (b) Brood weight. (c) Nymph weight (brood weight/ number of nymphs). (d) Proportion of viable eggs cannibalized in clutches. The parameters were measured at the sixth day after hatching (in the second instar). C: the control group in which clutches contained trophic eggs (n = 21). R: the trophic-egg removed group in which trophic eggs were removed from clutches (n = 22). Means and standard deviations are shown.
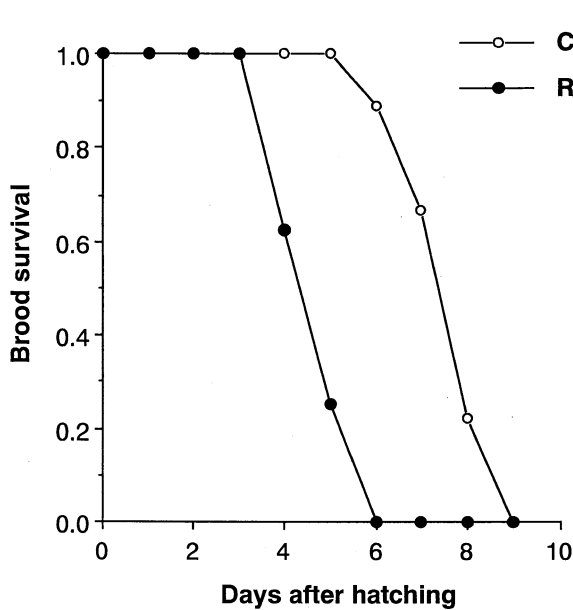

Fig. 3. The survivorship curves of broods in the trophic-egg removal experiments under seed-excluded conditions. C: the control group in which clutches contained trophic eggs (n = 9). R: the trophic-egg removed group in which clutches contained no trophic eggs (n = 8). The survivorship curves were based on individuals which lived longest in each of the broods.

Adomerus triguttulus nymphs depend on fallen mint seeds, and the production and distribution of the seeds varies greatly over small spatial scales and also changes temporally in the field habitat (Nakahira 1992). Despite maternal provisioning of seeds (below), female parents may sometimes be unsuccessful in carrying sufficient numbers of seeds to support their nymphs and the nymphs may suffer a shortage of food. Nymphs independent of their mother have to forage for host seeds scattered on the ground, which would be costly for the nymphs (Filippi et al. 2000). Selection presumably favours offspring possessing high mobility at independence from maternal care. Large resource-investment in individual offspring is required to accomplish such tolerance to food-shortage and high mobility (reviewed by Clutton-Brock 1991, Fox and Czesak 2000). Trophic-egg production, as well as parental provisioning of host seeds, must be adaptive under variable and risky environments.

Trophic eggs possibly have function(s) other than nutrition for hatched nymphs in *Adomerus triguttulus*. In some neuropterans, it is suggested that trophic eggs also function as a protective barrier against arthropod predators approaching viable eggs (Henry 1972). *Adomerus triguttulus* females add trophic eggs onto the cluster of viable eggs during care (Nakahira 1994). As a

consequence, the trophic eggs are situated on the surface of the clutch. In clutches collected in the field, eggs on the surface were sometimes crushed, probably due to predation (Nakahira 1992). Trophic eggs may reduce the predation risk to viable eggs from small arthropods.

The present results suggest that trophic eggs are maintained as extended parental investment in *A. triguttulus* (icebox hypothesis: Alexander 1974, Polis 1984). However, this hypothesis can not explain why female parents do not make larger viable eggs instead of producing trophic eggs separately (Crespi 1992). The loss of resources during feeding and the digestive process inevitably involves trophic-egg consumption by siblings. Sibling rivalry and parent–offspring conflict could be potentially operating in the *A. triguttulus* system. However, even when there were no available trophic eggs, hatched nymphs fed only minimally on viable eggs. There was no difference in the proportion of viable eggs eaten between broods with and without trophic eggs. There was no evidence indicating cannibalism among hatched nymphs within a brood: cannibalism among the nymphs was not observed during the experiments, and no difference in survival between broods with and without trophic eggs was detected. Parent–offspring conflict is, therefore, not expressed as sib-cannibalism in the current system. This suggests that maternal manipulation limits interactions among siblings. Hatching asynchrony generally enhances egg cannibalism within clutches (Baur and Baur 1986). *Adomerus triguttulus* females usually lay viable eggs within the first oviposition day (Nakahira 1992, 1994) and the high hatching synchrony resulting from such an oviposition mode could proximately prevent sib-cannibalism. In fact, when viable eggs with less embryonic development, which are prepared experimentally, are available, hatched nymphs feed upon them indiscriminately (Nakahira and Kudo, unpubl.).

The two hypotheses concerning the evolution of trophic eggs, extended parental investment (Alexander 1974, Polis 1984) and the solution of parent–offspring conflict under sibling oophagy (Crespi 1992), are not always mutually exclusive. In *A. triguttulus*, as mentioned above, large resource-investment in individual offspring (i.e. large eggs) would be favoured under variable and risky resource-environments. However, the body cavity of females could limit the total complement of eggs in the optimal size in single oviposition events. In *A. triguttulus*, viable-egg mass exceeds half of the female weight before oviposition (Nakahira 1994) and gravid females show extremely swollen abdomens, suggesting such a morphological constraint. In the ancestral state before the establishment of trophic eggs, large clutches consisting of large viable eggs may have been successively produced during a long oviposition period. This would inevitably induce hatching asynchrony within clutches and consequently sib-cannibalism. Conflicts would have

occurred in optimal oophagy rates between female parents and cannibal hatchlings. Selection must have favoured females to make some eggs inviable and less costly (Crespi 1992) and to produce viable eggs first and lay them within a short period. Females can add another protective function to trophic eggs through this oviposition mode, as well as control sibling cannibalism of viable eggs and the conflict over it. Moreover, despite the benefit to hatchlings, large viable eggs may increase the period for embryonic development and suffer high risk of predation or other environmental threats during the embryonic period (safe harbour hypothesis: Shine 1978; Sargent et al. 1987). Trophic-egg production would be favoured under such a situation because it is an effective way of providing nutritional resources to individual offspring without increasing the egg size and thus the embryonic period.

Trophic eggs in *A. triguttulus* are specialized and seem to cost less to produce as suggested by Crespi (1992); they are usually smaller than viable eggs and have a different chorion structure, lacking micropyles (Kudo et al. unpubl.). This is common to trophic eggs reported in other taxa (Henry 1972, Gobin et al. 1998). However, less investment in some eggs within a clutch could occur in a different ecological context. Where there is variation in predation risk among offspring within a clutch, less investment in offspring facing higher risk would be favoured (Temme 1986, Haig 1990, Mappes et al. 1997, Kudo 2001). *Adomerus triguttulus* trophic eggs, which are situated on the surface of the clutch and thus suffer high predation, could also be regarded as an extreme case of such unequal parental investment. Pre-existed unequal investment within clutches may have promoted the evolution of trophic eggs in its origin, as well as the parent–offspring conflict under sibling oophagy.

On the other hand, females also suffer fecundity costs through trophic-egg production; if all eggs were viable, brood size would increase greatly. The increased parental investment in terms of trophic-egg production may also impose costs on female future survival (Roff 1992, Stearns 1992). It is most likely that the optimal trophic-egg production for females (and for offspring) depends on their own conditions and/or environmental resource availability (Osawa 1992). In *Adomerus triguttulus*, female phenotype affected the allocation of trophic eggs and viable eggs; larger females produced clutches consisting of more viable eggs with relatively fewer trophic eggs. Why do they show such allocation?

As in other sub-social cydnid bugs (Filippi et al. 1995, Kight 1997, Agrawal et al. 2001), *Adomerus triguttulus* females show complex care behaviour, including defence against natural enemies and provisioning of host seeds for nymphs (Nakahira 1992, Kudo and Nakahira unpubl.). The body size of parents often affects brood care in insects (Mappes and Kaitala 1994, Reid and Roitberg 1995, Hunt and Simmons 2000, Kim and

Thorp 2001), and consequently may affect allocation of parental investment (Sargent et al. 1987, reviewed by Clutton-Brock 1991). The degree of seed provisioning varies greatly among *A. triguttulus* broods (Nakahira and Kudo, unpubl.), possibly in response to female body size. If small females are poor seed-collectors, they could compensate for this by producing more trophic eggs. Another possible function of trophic eggs, a barrier against predators, could also affect their allocation. In spherical clutches, the surface to volume ratio decreases with increasing volume; larger clutches with more viable eggs have relatively smaller surface areas. Trophic eggs that cover the surface of clutches may thus decrease with the number of viable eggs.

As well as functional explanations of trophic eggs as extended parental investment, another view, in which trophic eggs play a role in resolving parent–offspring conflict under sibling oophagy, might explain the variation of trophic-egg allocation among clutches. Parker and Mock' (1987) model, which analysed parent–offspring conflict over clutch size under sibling cannibalism, predicted that larger clutches could reduce the conflict where offspring kill a fixed number of siblings. This theory may explain lower trophic-egg ratios in larger clutches of *Adomerus triguttulus*; larger clutch production could represent an alternative solution by females to the conflict instead of trophic-egg production. As previously mentioned, however, this explanation would not meet the case of *Adomerus triguttulus*; parent–offspring conflict is not expressed as sib cannibalism in the current system, and thus trophic eggs do not seem to be maintained in a role of conflict-solution by females.

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