
Trophic egg laying: hypotheses and tests

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Trophic egg-laying – wherein mothers provide non-developing eggs for offspring to eat – has attracted much empirical attention to diverse taxa (e.g. amphibians, non-social and eusocial insects, fish, and marine gastropods). However, there has been only a limited exchange of ideas among studies of different taxa. We advocate a unified approach to the study of trophic eggs within an evolutionary ecological framework. In this paper, we stress the importance of elucidating the adaptive function of trophic eggs through explicit hypothesis testing, and our primary objective is to outline key experiments that can test adaptive and functional hypotheses. Currently, some cases of hypothesized trophic eggs may simply represent offspring consumption of eggs that failed to develop for non-adaptive reasons (e.g. sperm limitation). Furthermore, in many trophic egg-laying species, it is unclear whether trophic eggs have evolved to provision offspring or to reduce cannibalism among offspring. With increased focus on theory and hypothesis testing, the study of trophic eggs can offer important insight into topics such as sibling rivalry, parent-offspring conflict, and parental care.

Trophic eggs (also called nurse eggs) are non-developing eggs or egg-like structures produced for offspring consumption (Crespi 1992). Trophic egg laying occurs with diverse parental care systems (including no care) and with or without offspring cannibalism of viable siblings. In some species, embryonic offspring eat thousands of eggs in utero (e.g. the sand tiger shark *Odontaspis taurus*, Wourms et al. 1988). In others, newly emerged offspring consume non-developed eggs within their natal egg batch (e.g. the ladybeetle *Harmonia axyridis*, Perry and Roitberg 2005b). Mothers may also lay trophic eggs while tending to offspring (e.g. the burrower bug *Adomerus triguttulus*, Kudo and Nakahira 2004) or repeatedly visiting offspring (e.g. Beebe's rocket frog, *Colostethus beebei*, Bourne et al. 2001). Hence, although these species vary immensely in ecology and life history, they apparently share an extraordinary maternal tactic: reassigning the ovarian machinery to produce food for their young, while sometimes risking the loss of viable offspring.

By the 1920s, studies had emerged reporting offspring consumption of non-developing eggs in sharks (Shann 1923) and non-social insects (Hawkes and Marriner 1927). Until the 1980s, however, trophic eggs were typically noted in passing in descriptive studies of the reproductive ecology of fish, Amphibia, insects, spiders, spionid worms and prosobranch snails. Trophic egg laying attracted increasing attention in the 1980s (particularly in studies of frogs, prosobranchia and spiders), with the appearance of observational and experimental studies devoted solely to trophic eggs. The pace of trophic egg research has accelerated in past decades, and there are now 142 studies citing the keywords trophic egg* or nurse egg* (Aug. 2005, BIOSIS Previews).

Although a substantial empirical literature has accumulated, the bulk of current trophic egg research simply describes maternal and offspring behaviours. Hence, two important questions are often unresolved. (1) For a given species, are hypothesized trophic eggs an evolved maternal phenotype or simply failed byproducts (due to, for example, gamete incompatibility or sperm limitation)? Because this question is not generally asked, the prevalence of trophic egg-laying across species is currently unclear. (2) If trophic eggs are an adaptive phenotype, in what particular context are they adaptive? Trophic eggs may function to provision offspring (Alexander 1974) or to reduce sibling cannibalism (Crespi 1992). There is currently a lack of theory to inform the conditions in which either hypothesis is plausible; this deficiency must also be addressed for the field to move forward.

Our primary goal here is to outline an evolutionary ecological approach to the study of trophic eggs, based on the two questions above concerning the adaptive value and function of hypothesized trophic eggs. Our emphasis is on hypotheses that address the two questions and methods for testing them. With respect to question 1, we categorize trophic egg-laying species by whether

they exhibit a complex trophic egg phenotype (indicating a phenotype that has been selected for some function) or not. For those that do not, we outline tests of the trophic egg vs byproduct hypotheses. To address question 2, we introduce an inclusive fitness theory that delineates the two main functional hypotheses (provisioning vs reduction of cannibalism). Throughout the paper, we promote a conceptual unification of trophic egg research – which is currently conducted in taxonomic isolation – by highlighting examples from a wide variety of taxa. We focus on non-eusocial taxa since eusocial trophic eggs have been reviewed by Crespi (1992).

An evolutionary ecological approach to trophic eggs

Question 1. Are the hypothesized trophic eggs an evolved phenotype?

By Crespi's (1992) definition, trophic eggs are an evolved maternal phenotype, not simply unavoidable non-developing eggs that happen to be eaten by offspring. This distinction is not trivial. Hypotheses for the function of trophic eggs can be devised and tested (as addressed in the following section), whereas haphazard non-developing eggs are functionless. Hence, a study of putative trophic eggs should first test the trophic vs byproduct hypotheses. In some species the evolutionary precursors to trophic eggs may be haphazard infertile eggs. If selection has modified such infertile eggs to facilitate their consumption by offspring, then it is reasonable to consider the eggs as trophic.

For some species – those in which there is a complex trophic egg phenotype – the appearance of adaptation seems clear; that is, in which trophic eggs themselves, or the associated maternal behaviours, appear obviously fine-tuned for facilitating egg-consumption by offspring. Such specialization reveals the signature of natural selection (Williams 1966, Thornhill 1990, Reeve and Sherman 1993). In these species, it is reasonable to reject the byproduct hypothesis and proceed directly to testing trophic egg function. Examples of specialized phenotypes include trophic eggs that are morphologically or biochemically distinct from other eggs in a way that is seemingly specialized to offspring needs; or mothers that, by their behaviour, appear to make a concerted effort to produce and/or distribute trophic eggs (Table 1). The trophic eggs of many frogs, eusocial insects, and several sub-social insects, spiders and gastropods illustrate obvious specialization.

In many species, hypothesized trophic eggs are distinct from other eggs and occur with no specialized delivery behaviours (Table 1). Without obvious specialization, testing the trophic egg hypothesis through experimentation is essential. Most non-social insects

and several fish, spiders and polychaete worms fit this category.

Testing the trophic egg vs byproduct hypotheses

We suggest three approaches to resolving the trophic egg and byproduct hypotheses, for animals without an obviously finely-tuned trophic egg phenotype that suggests that selection has promoted trophic egg eating.

First, in some species a specialized trophic egg phenotype will become apparent only upon close observation or experimentation. The trophic egg hypothesis is supported if any of the following five characters are found, though the absence of any character does not falsify the hypothesis:

- *Mass quantity.* In some species, so many seemingly trophic eggs are consumed by offspring that it is reasonable to conclude that they are not failed byproducts. For example, embryonic sand sharks (*Odontaspis taurus*) consume tens of thousands of eggs (up to 24 000) in utero (Springer 1948, Gilmore et al. 1983). The trophic egg hypothesis could be dismissed if, in related sharks, equally many non-developing eggs are produced but not eaten by embryonic offspring.
- *Specialized cellular development.* The trophic eggs of some species display a specialized cessation of development, distinct from other non-developing eggs. As examples, the trophic eggs of *Boccardia proboscidea* (Polychaeta: Spionidae, Smith and Gibson 1999) and eusocial Hymenoptera (Voss et al. 1987) undergo active cell death. In *B. proboscidea*, trophic egg yolk also becomes compartmentalized into easily swallowed vesicles (Smith and Gibson 1999).
- *Costly trophic eggs.* Trophic eggs may be relatively costly if they are larger or richer in lipids and proteins than other eggs, implying that they are specialized to offspring nutritional requirements. Relative costs for viable and trophic eggs could be compared directly by mass, calorimeter measurements and lipid-protein analysis. Alternatively, cost could be tested by experimentally assessing the tradeoff between production of trophic and viable eggs. A tradeoff may be observed as a change in the absolute number of eggs laid as a function of the ratio of viable to trophic eggs. One might examine the tradeoff over the natural variation in numbers of trophic eggs, but this relationship may be confounded if mothers modify trophic egg production according to their condition. Alternatively, one can induce variation in trophic egg numbers (e.g. by 'informing' mothers of resource conditions for offspring). In many systems, however, it will be difficult to provide such information without affecting maternal condition. To date, no study has examined the relative cost of trophic eggs.

Table 1. Taxa that produce (hypothesized) trophic eggs – non-developing eggs consumed by offspring. In some species (a), there is no specialization of hypothesized trophic eggs or maternal delivery behaviours. Without further evidence, it is not clear whether such eggs are trophic eggs or failed non-developing eggs. In others species (b), trophic eggs themselves or the associated maternal behaviours show fine-tuning for feeding offspring. Species for which specialization of egg and maternal behaviours are not known are excluded, including several polychaete worms and many gastropods. Eusocial species in which trophic eggs are fed to larvae are included; in many others, workers or queens eat trophic eggs, possibly an outcome of reproductive conflict. Question marks indicate that the factor was not discussed in the study.

(a) Species (Family)	Sibling cannibalism?	Notes	Source	
Vertebrates				
<i>Salamandra atra</i> (Salamandridae)	–	intrauterine	Dopazo and Alberch 1994	
<i>Alopias superciliosus</i> (Alopiidae)	+	intrauterine	Gruber and Compagno 1981	
<i>Delphyodontos dacriformes</i> (extinct; Chondrichthyes)	?	intrauterine	Lund 1980	
<i>Lamna cornubica</i> (Lamnidae)	?	intrauterine	refs in Wourms 1977	
Insects				
Various ladybird beetles (15 species; Coccinellidae)	+		Osawa 2003, Michaud and Grant 2004	
Various lacewings (Chrysopidae)	+		refs. within Hinton 1981, Frechette and Coderre 2000	
<i>Labidomera clivicollis</i> (Chrysomelidae)	+		Dickinson 1992	
<i>Oncopeltus</i> spp. (Lygaeidae)	+		Root and Chaplin 1976	
Other invertebrates				
<i>Arianta arbustorum</i> (Helicidae)	+		Baur and Baur 1998	
Several polychaete worms (Spionidae)	?	occurs within egg capsule	refs in Blake and Arnofsky 1999, MacKay and Gibson 1999	
Several spiders (Theridiidae, Clubionidae, Gnaphosidae, Scytodidae)	– (Theridiidae, Clubionidae); ? (other families)	occurs within egg sac	Kaston 1970, Peck and Whitcomb 1970, Valerio 1974, Downes 1985	
(b) Species (Family)	Sibling cannibalism?	Trophic eggs (TEs) distinct?	Specialized TE delivery behaviour in parents?	Source
Vertebrates				
Various tree frogs (at least 17 species; Dendrobatidae, Hylidae, Leptodactylidae, Mantellidae, Rhacophoridae)	–	–	+ (repeated TE laying)	refs in Crump 1996, Kam et al. 2000, Heying 2001, Gibson and Buley 2004
<i>Bagrus meridionalis</i> (Bagridae)	?	?	+ (repeated TE laying)	McKaye 1986
<i>Carcharias taurus</i> (Odontaspidae)	?	+	+ (continually supplied TEs in oviduct)	Springer 1948, Gilmore et al. 1983, Wourms et al. 1988
<i>Latimeria chalumnae</i> (Coelacanthidae)	?	?	+ (continually supplied TEs in oviduct)	Wourms et al. 1991
Insects				
<i>Adomerus triguttulus</i> (Cydnidae)	+	+	+ (repeated TE laying)	Nakahira 1994, Kudo and Nakahira 2004
<i>Anurogryllus muticus</i> (Gryllidae)	–	+	+ (repeated TE laying)	West and Alexander 1963
<i>Ascaloptynx furciger</i> (Ascalaphidae)	–	+	–	Henry 1972
Other invertebrates				
Several polychaete worms (Spionidae)	?	+	?	refs in Blake and Arnofsky 1999, Smith and Gibson 1999
<i>Amaurobius ferox</i> (Amaurobiidae)	–	?	+ (laid after offspring hatch)	Kim and Roland 2000
<i>Amaurobius fenestralis</i> (Amaurobiidae)	?	–	+ (laid after offspring hatch)	Gundermann et al. 1991
<i>Coelotes terrestris</i> (Agelenida)	?	?	+ (laid after offspring hatch)	Gundermann et al. 1991

Table 1 (Continued)

(b) Species (Family)	Sibling cannibalism?	Trophic eggs (TEs) distinct?	Specialized TE delivery behaviour in parents?	Source
<i>Diaea ergandros</i> (Thomisidae)	+	+	+	Evans et al. 1995
Several prosobranch gastropods (Buccinidae, Calyptraeidae, Melongenidae, Muricidae)*	+/-	+	+	refs in Thorson 1950, Rivest 1983, Gallardo and Garrido 1987, Morton 1987, González and Gallardo 1999
Eusocial insects				
Various ants (Formicidae); queen-produced trophic eggs	+	+	+	Gobin and Ito 2000, Cassill 2002, Masuko 2003
Various ant (Formicidae); worker-produced trophic eggs	-	+	+	Gobin et al. 1998, Heinze et al. 1999, Gobin and Ito 2000, Dijkstra et al. 2005

* Occasionally observed in one species (*Searlesia dira*; Rivest 1983)

- *Distribution*. An over-dispersed distribution of trophic eggs would be difficult to explain by the byproduct hypothesis, and may maximize offspring consumption of trophic eggs instead of viable eggs. Non-random distribution was tested, though not detected, in the ladybeetle *Harmonia axyridis* (Perry and Roitberg 2005b).
- *Adaptive plasticity*. Mothers may show adaptive plasticity in laying trophic eggs or in adjusting their number according to environmental conditions. For example, female *Amaurobius ferox* and *Coelotes terrestris* spiders lay trophic eggs if offspring are present, but viable eggs if offspring are removed (Gundermann et al. 1991, Kim and Roland 2000). In some tree frogs, females require physical contact with offspring before depositing trophic eggs into the small pools where offspring are confined (Jungfer 1996). And in other species, mothers adjust the number of trophic eggs based on the number of offspring (e.g. a rhacophorid frog, Kam et al. 1998), offspring age (e.g. a leptodactylid frog, Gibson and Buley 2004) or starvation risk. In testing whether trophic egg production increases with greater offspring starvation risk, empiricists must ensure that maternal information state (low or high risk for offspring) is not confounded with maternal condition, and that the range of environments tested is great enough to capture a switch in maternal tactic. This can be particularly difficult when both parents and offspring exploit the same resources. Studies have tested this prediction in the laboratory; trophic egg plasticity was detected in *H. axyridis* (Perry and Roitberg 2005b) but not in the lacewing *Chrysoperla rufilabris* (Frechette and Coderre 2000). Across natural habitats that differed in offspring starvation risk, no plasticity was detected in a leaf beetle (Dickinson 1992) or a land snail (Baur and Baur 1998).

In a second approach, three comparative predictions could resolve the trophic egg and byproduct hypotheses. First, in species without egg-eating offspring, any non-developing eggs must certainly be a byproduct of constraints on egg maturation. If related species with egg-eating offspring have a similar proportion of non-developing eggs, then the trophic egg hypothesis can be rejected in these species as well. On the other hand, if species with egg-eating offspring tend to produce more non-developing eggs, then it is difficult to accept the trophic egg hypothesis without reservations because causation is not clear: perhaps egg-eating is most likely to evolve in species with a high rate of failed eggs.

Non-developing (hypothesized trophic) eggs should be more common in species that encounter high food availability during egg formation but low food during parental care or offspring foraging, compared to species

that encounter other temporal food patterns (Alexander 1974, Polis 1981, Mock and Forbes 1995, Mock and Parker 1997). The implication, then, is that mothers store food for offspring as trophic eggs. A related prediction is that if non-developing eggs are really trophic eggs, then the proportion of non-developing eggs will be higher in populations or species in which offspring experience higher starvation risk than in low-risk groups. In a test of this prediction, populations of a leaf beetle (*Labidomera clivicollis*) that differed in starvation risk did not differ in production of infertile eggs, implying that such eggs are simply failed byproducts (Dickinson 1992). Save for this last result, there have been no comparative analyses of trophic egg laying with the goal of elucidating adaptive value.

A third potential approach is to test the byproduct hypothesis directly by varying factors that may cause egg development to fail, such as sperm availability or oxygen concentration, to test for an effect on the production of non-developing eggs. If such an effect is evident, then it is worth considering how much variation in the proportion of non-developing eggs is explained. Some fraction may be produced by constraint while an additional portion is adaptively produced. For example, in the marine gastropod *Acanthina monodon*, an experimentally elevated oxygen level increased the proportion of developing eggs (Lardies and Fernández 2002). Yet it is doubtful that all of the non-developing eggs in this species are due ultimately to lack of oxygen because embryos require nutrition from these eggs to complete development (Gallardo 1979), indicating that their production is an evolved maternal phenotype.

Finally, we note an approach that cannot distinguish the trophic egg and byproduct hypotheses. The observation that mothers receive a net benefit from offspring consumption of eggs does not permit the conclusion that the eggs are trophic (as in Osawa 1992). Some benefit from eating eggs is expected – else offspring would presumably refrain from eating eggs – but measurable benefit does not demonstrate that mothers use any tactic to facilitate egg eating.

Question 2. What is the adaptive function?

For our purposes, an adaptation is a phenotypic variant with highest fitness, relative to plausible alternatives, in a specified environmental context (following Reeve and Sherman 1993). For most studies of trophic eggs, a reasonable metric for fitness is the lifetime number of offspring that survive to maturity. The set of alternative phenotypes should include the absence of trophic eggs and varying numbers of trophic eggs, higher and lower than the species average. This definition of adaptation, and the related research programme that we discuss below, can elucidate the function of seemingly adaptive

trophic egg laying. In some cases, one can gain insight into adaptive function by simply characterizing the environmental context (e.g. food availability) in which trophic eggs are produced. However, without measuring fitness, it may still be unclear whether the specific quantity of trophic eggs laid is the most adaptive phenotype.

The two possible functions for trophic egg laying – provisioning offspring or reducing sibling cannibalism – are expected in contrasting environmental contexts, distinguished by the level of starvation risk that offspring face. In a relatively high starvation risk environment, provisioning offspring is the plausible function, whereas with intermediate starvation risk, cannibalism reduction is more likely (Perry 2004, Perry and Roitberg 2005a). Consider that cannibalism is favoured for offspring when the relative benefit of cannibalism (RBC; i.e. the increase in survival that cannibals experience, relative to the victim's probability of survival if not cannibalized) is greater than the coefficient of relatedness, r , among siblings (Eickwort 1973). (This threshold is lower than the coefficient of relatedness if there is competition among cannibal offspring (Perry and Roitberg 2005a), but this new result does not change the substance of our argument here.) Parents, on the other hand, benefit from cannibalism among their offspring only when the $RBC > 100\%$ (O'Connor 1978).

In environments of high starvation risk (measured by RBC values exceeding 100%), parental and offspring interests coincide in agreement that cannibalism should proceed. In this case, mothers benefit from sacrificing some offspring to others, e.g. by laying a trophic egg. This is the provisioning hypothesis – that trophic eggs serve to provide offspring with energy (Alexander 1974, Polis 1981, Crespi 1992, Pfennig 1997, Perry 2004) or a limiting nutrient (e.g. protein, Polis 1984, or calcium in gastropods, Baur 1990). In contrast, parents and offspring conflict over cannibalism when there is intermediate starvation risk (RBC values from $r\%$ to 100%). Here, mothers should adopt strategies to limit cannibalism, e.g. producing trophic eggs that are less costly than viable eggs but that provide enough energy that offspring refrain from eating viable siblings (the cannibalism reduction hypothesis, Crespi 1992). Models are required to predict whether such a solution is evolutionarily stable when maternal and offspring interests conflict. Thus, trophic egg laying may be adaptive in both high and low starvation risk environments but would serve different functions in each context. In fact, because there is a threshold switch in optimal parental behaviour with regard to facilitating or limiting cannibalism among offspring, trophic egg laying cannot serve both functions at the same time in a given system.

Though a parental threshold for favouring cannibalism among offspring is expected, whether the threshold

value is 100% depends on the tradeoff in production of trophic and viable eggs. In some species, the tradeoff appears to be one-to-one: both egg types are produced at the same time and are about the same size and composition (e.g. in coccinellid beetles, Perry and Roitberg 2005b). For those species, mothers should only trade trophic for viable eggs when $RBC > 100\%$. In other species, mothers probably do not trade a viable egg for every trophic egg produced – for example, when trophic eggs are laid after viable eggs (e.g. in burrower bugs, Kudo and Nakahira 2005) or trophic eggs are smaller than viable eggs or contain fewer costly lipids and proteins (e.g. in burrowing crickets, West and Alexander 1963). For these species, if $RBC < 100\%$, then the optimal maternal strategy is not clear. Even if offspring do not cannibalize siblings, it may still benefit mothers to produce trophic eggs, depending on their cost relative to viable eggs. Again, there is a need for models of optimal trophic egg strategy for differing tradeoff functions.

When should trophic egg-laying evolve, as opposed to alternative tactics? Several authors have suggested that trophic egg-laying should evolve only when egg size is constrained (Polis 1984, Mock and Parker 1997, Dixon 2000). Increased egg size may necessitate larger ovarioles and possibly a larger body size; thus, in some species, trophic eggs may be the best alternative. Moreover, it may be difficult for mothers to facultatively adjust egg size across oviposition sites that vary in food availability; e.g. in many insects mothers may be unable to adjust yolk investment late in egg maturation (Kudo and Nakahira 2005). Egg development may be easier to adjust (e.g. by fertilizing or not fertilizing eggs). A second alternative tactic is for mothers to facilitate or limit sibling cannibalism by manipulating hatching synchrony within clutches (Godfray 1987, Baur and Baur 1998). Eggs that happen to go uneaten could continue development into viable offspring. Trophic egg laying may be advantageous if mothers have imperfect control over hatching synchrony: it may be better to halt the development of some eggs to ensure that they become meals.

Other functions

Trophic eggs occasionally have hypothesized functions not related to offspring feeding. In eusocial Hymenoptera, reproductive conflicts of interest between queens and workers, or among workers, might explain worker-laid trophic eggs (Crespi 1992); this hypothesis remains an under-explored possibility (but see Gobin et al. 1998). In some species, trophic eggs may protect viable eggs from predators (Kudo and Nakahira 2004), or give embryonic offspring hunting experience before birth (Gilmore et al. 1983).

Testing functional hypotheses

Several methods would be useful for discriminating the provisioning vs cannibalism reduction hypotheses.

Relative benefit of cannibalism

As discussed above, if the RBC is consistently $> 100\%$, the provisioning hypothesis is supported, while if RBC is consistently $< 100\%$, the conflict reduction hypothesis is implied (at least for animals in which there is a 1:1 tradeoff between trophic and viable eggs, as per our comments above). An empirical challenge is to obtain RBC measures that reflect the resource conditions experienced both during the evolution of trophic eggs, and that capture temporal and spatial variation (Osawa 1992). It is therefore important to estimate the frequency distribution of resource environments that a species experiences and to measure RBC in the environments most commonly encountered. RBC values have been measured in several systems (compiled in Perry and Roitberg 2005a), though not, typically, to assess trophic egg function (except in Kudo and Nakahira 2004). Studies often calculate the survival value of eating an egg relative to starvation, or the benefit of eating many (often uncounted) trophic eggs; neither metric is useful for distinguishing the functional hypotheses.

Adaptive plasticity

According to the provisioning hypothesis, mothers would do best to adjust trophic egg production according to environmental context. Given that trophic egg laying should be most adaptive when offspring starvation risk is high, we expect mothers to lay trophic eggs when offspring starvation risk is high but to reduce or cease production when risk is low (Frechette and Coderre 2000, Perry 2004). Methods of testing for plasticity are described in the above Testing section. To exclude the cannibalism reduction hypothesis, researchers must ensure that sibling cannibalism does not also increase in high starvation environments. In many batch-laying insects, this possible confound can be dismissed, as offspring have no information about food levels before cannibalizing siblings (Dickinson 1992, Frechette and Coderre 2000).

Obligate trophic egg feeding

If offspring require trophic eggs for growth (as in numerous tree frogs, Weygoldt 1987, Brust 1993, Jungfer 1996, Kam et al. 1998, Gibson and Buley 2004), a provisioning function is clear. The alternative phenotype of no trophic egg production has zero fitness.

Trophic egg removal

The cannibalism reduction hypothesis predicts that if trophic eggs are removed, the rate of cannibalism among offspring should increase. If not, the cannibalism reduction hypothesis is falsified. However, an increase in

cannibalism among offspring is also consistent with the provisioning hypothesis, if offspring turn to siblings as food in the absence of trophic eggs.

Cost

If the function of trophic eggs is to reduce cannibalism in a given species, and if each trophic egg saves one offspring from cannibalism, then trophic eggs must be less costly to produce than viable eggs; else mothers help offspring avoid cannibalism at the cost of an equal number of potentially viable embryos. Trophic eggs that are less costly are consistent with provisioning or cannibalism reduction functions. Empirical approaches are discussed in the above Testing section.

In many species a provisioning function is clearly implicated (Table 1 lists species in which trophic egg feeding is obligate). A cannibalism reduction function has been explicitly suggested for several systems (Nakahira 1994, Kim and Roland 2000, Lardies and Fernández 2002), but only Kudo and Nakahira's (2004) study of the burrower bug *A. triguttulus* had the explicit goal of distinguishing the provisioning and cannibalism reduction hypotheses.

In *A. triguttulus*, females care for offspring until the second instar, providing protection and nutlets (small fruits) as food. After laying viable eggs, mothers oviposit non-developing eggs on top of viable eggs. Upon hatching, offspring consume the inviable eggs as well as some unhatched siblings. Clearly the non-developing eggs are trophic: there is specialization in the timing and location of oviposition, and they are not simply unfertilized but have a different chorion structure than viable eggs (Kudo and Nakahira 2004). To test the provisioning vs cannibalism reduction hypotheses, Kudo and Nakahira (2004) removed mothers after oviposition of viable eggs (preventing trophic egg-laying) or allowed mothers to remain with eggs. Offspring growth and survival and the frequency of sibling cannibalism were then measured in high and low food (nutlet) conditions. The presence or absence of trophic eggs did not affect the rate of sibling cannibalism, which was low in both treatments. This result suggests that the trophic eggs of *A. triguttulus* do not function to reduce sibling cannibalism, making provisioning the likely alternative.

Summary and future prospects

Trophic egg studies now have a solid base of descriptive data from many taxa. However, progress on the evolutionary ecology of trophic egg laying appears stalled. Here, we have suggested a number of research methods that can aid the advancement of trophic egg studies. We have emphasized the need for adaptive and functional hypothesis testing, and identified specific areas where a

dearth of theory now exists. Our hope is that trophic egg research can move forward under a unified framework, and as such may benefit from the taxonomic diversity in which this unique phenotype exists.

The concepts we have discussed may be extended to consider trophic offspring – those offspring produced for consumption by other offspring. Trophic offspring may occur when mothers facilitate cannibalism among offspring; potential examples include land snails (Baur 1990, Baur and Baur 1998) and ladybird beetles (Osawa 1992).

Many prospects remain for trophic egg research. The first major challenge is to identify ecological and life history factors correlated with trophic eggs in order to explain their evolution in some taxa and absence in others (Lyons and Spight 1973, Crump 1992). Several comparative hypotheses have been discussed but none have been tested. For example, trophic eggs may evolve in species that experience abundant food during offspring creation but limited food during parental provisioning or offspring foraging (the icebox hypothesis, Alexander 1974, Mock and Forbes 1995, Mock and Parker 1997); in which egg size is constrained from increasing (Polis 1984); or in which offspring have limited ability to acquire or digest food (Ibarra N. 1985, McKaye 1986, Crespi 1992, Nakahira 1994, Kim and Roland 2000, Masuko 2003). We suspect that this last prediction has merit: Table 1 lists many species in which offspring have limited mobility (e.g. tree frogs, gastropods) or limited food-acquiring ability (e.g. neonate coccinellids, which are notoriously poor predators). Another future challenge is to identify the developmental mechanisms by which trophic eggs differentiate from viable eggs, which have been addressed only rarely in some eusocial insects (Voss et al. 1987), spionid worms (MacKay and Gibson 1999) and prosobranch gastropods (Gallardo and Garrido 1987). It would be of great interest to determine whether the cessation of development in trophic eggs is controlled by maternal or embryonic genes; if the latter, then trophic eggs may represent “a sterile caste destined to be cannibalized”, as Crespi (1992), p. 176) suggested. Finally, there is a need for clear evolutionary scenarios for the origin of trophic eggs and further modification of mother and offspring traits (Crespi 1992). Current work on the evolution of trophic eggs is limited to hypotheses on the evolution of parental care behaviours in tree frogs (Weygoldt 1987, Jungfer and Weygoldt 1999, Bourne et al. 2001).

Trophic egg studies may be a testing ground for many unresolved questions in evolutionary ecology. For example, bet-hedging strategy is currently an area with an abundance of theory in need of empirical attention (Hopper 1999, DeWitt and Langerhans 2004). Trophic eggs may operate as a bet-hedging strategy in some species by generating variation in offspring size and

permitting the largest offspring to survive even poor food conditions (Rivest 1983, Osawa 1992, Chaparro et al. 1999, González and Gallardo 1999, Kudo and Nakahira 2004), which may reduce variation in parental fitness. The bet-hedging hypothesis for trophic eggs has yet to be tested against the alternative hypothesis of a single optimum in provisioning per offspring. Another important empirical question is how spatial and temporal variation can select for phenotypic plasticity (Doughty and Reznick 2004). Species that exhibit plasticity in trophic egg production may be useful study systems (e.g. *H. axyridis*, Perry and Roitberg 2005b) to address the question. More generally, we hope that future research on trophic egg laying can offer unique and valuable insights into parental care, parent-offspring conflict, and sibling rivalry.

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