Chapter 8
Future Directions: Where Do We Go from Here?

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Abstract In recent years, six species within the Superfamily Sehirinae that progressively provision seeds/drupes/nutlets to their young have been identified, one cydnid in North America and four cydnids and *Parastrachia japonensis* (Parastrachiidae) in Japan. This chapter begins with a reflection on some of the similarities and differences among the members of this parental cluster. It then considers the various directions that future research on *P. japonensis* should take, such as comparison of the life history with that of *P. nagaensis*, clarification of the ecological factors that regulate the proportion of individuals that refrain from mating until the second spring, and the mechanism of symbiont transfer that makes the 2-year lifespan without feeding possible. We refer to the questions that remain about mating behavior, regulation of trophic egg production, and parent-offspring communication, as well as the need for further exploration on navigation behaviors, particularly the mechanisms used at night. Finally, we stress the need for studies to confirm unpublished findings presented in this chapter regarding suppression of sibling cannibalism while the female is away from the nest.

Keywords Cannibalism · Cydnidae · Parent-offspring conflict · Mating behavior · Navigation · Parastrachiidae · Provisioning insects · Sibling rivalry · Symbionts · Trophic eggs

8.1 Introduction

Our first public announcement about the remarkable progressive provisioning behavior of *P. japonensis* took place over 30 years ago at the 35th Annual Conference of the Japanese Society of Applied Entomology and Zoology. We were quite

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excited to be presenting our findings and were certain the news about the first evidence of a phytophagous terrestrial heteropteran that progressively provisioned young would be the hottest topic at the conference! Well, that was until we discovered through the conference buzz that Taiichi Nakahira from Hokkaido University, who was equally excited about presenting what he thought was going to be a first-ever discovery, was planning to present very similar findings about his research organism, a cydnid, *Adomerus triguttulus* (Nakahira 1991). It is fair to say that we were both just a tad deflated when we found out about each other's discovery, but nevertheless rose to the occasion, and our respective stories were well-received. Since that time, and to our delight, research in the Nomakuchi Animal Behavioral Ecology laboratory at Saga University has revealed similar parental care behaviors in three additional Japanese cydnid species, *Adomerus rotundus* (Inadomi et al. 2014), *A. variegatus* (Mukai et al. 2010), and *Canthophorus niveimarginatus* (Filippi et al. 2009).

8.2 Similarities and Differences Among Members of the Parental Cluster

The three cydnid species investigated by the Nomakuchi laboratory display similar parental care behaviors to *A. triguttulus*, *P. japonensis*, and the single North American representative of this cluster, *Sehirus cinctus* (Sites and McPherson 1982; Kight 1997). They all have egg-guarding and progressive provisioning; however, there are differences in the patterns of when provisioning begins. Mothers of some species repeatedly leave the nest during the guarding phase to feed, while others never feed during this phase (Table 8.1). One species begins provisioning at the second nymphal stadium, while others begin soon after hatch. A non-parental cydnid, *Adrisa magna*, drags drupes to a sheltered site and feeds in solitary and in aggregations in the laboratory (Takeuchi and Tamura 2000), and LF has observed other unidentified Japanese and American cydnids transporting seeds to feed under leaves in the field. This behavior of transporting drupes to a sheltered site would minimize the risks of conspecific competition and predation while feeding and could be a preadaptation for progressive provisioning.

There is also variation in parity among the species. *Parastrachia japonensis* is unique among this club of provisioning cydnids in its obligate semelparity (Table 8.1; Filippi et al. 2002), which is likely a response to the severe constraint presented by the fickle food resource. Obligate semelparity indicates that the selective pressure for effective provisioning is much greater in *P. japonensis* than it is in the provisioning cydnids which have multiple opportunities to reproduce.

Additionally, the five cydnids provision very tiny seeds, certainly tiny relative to their body size (Fig. 8.1). The winged seed that *A. variegatus* provisions is somewhat more cumbersome than the other mint seeds; however, the female drags it along behind its body so that it does not interfere with walking (Fig. 8.1b), and the overall

Table 8.1 Comparison of parameters related to trophic egg production and timing of provisioning in parental bugs

Species	Parity	Mother leaves eggs to feed	Pre-hatch trophic eggs	Post-hatch trophic eggs	Resource constraint	Predation risk	Reference
Parastrachia japonensis	Semelparous	No	Yes	No	Yes, severe	Yes	Hironaka et al. (2005)
Adomerus triguttulus	Iteroparous	Yes	Yes	No	No	Yes	Kudo and Nakahira (2004)
Adomerus rotundus	Iteroparous	No	Yes, but very few	Yes	No	Yes	Inadomi et al. (2014)
Adomerus variegates	Iteroparous	No	Yes, but very few	No	Yes, moderate-severe	Yes	Mukai et al. (2010)
Canthophorus niveimarginatus	Iteroparous	No	Yes	Yes	Yes, moderate	Yes	Filippi et al. (2009)
Sehirus cinctus	Iteroparous	Yes, in lab	No	No	No	Yes	LF, pers. observations in lab

Fig. 8.1 Seed provisioning subsocial bugs. (**a**) *Adomerus triguttulus* transporting deadnettle (*Lamium* spp.) seed*;* (**b**) *A. variegatus* transporting winged seed of Japanese elm (*Ulmus davidiana*)*;* (**c**) *P. japonensis* transporting (*Schoepfia jasminodora*) drupe*;* (**d**) *A. rotundus* transporting (*Lamium amplexicaule*) seed; (**e**) *Canthophorus niveimarginatus* transporting kanabiki-sou (*Thesium chinense*) seed*;* (**f**) *Sehirus cinctus albonotatus* transporting purple deadnettle (*Lamium purpureum*) seed. (**a**, **b**, **d**, **e**) Photo credit, Mantaro Hironaka

weight difference pales in comparison to the unwieldy and heavy drupes that *P. japonensis* females provision (Fig. 8.1c). Agrawal et al. (2005) concluded that the cost of the provisioning component of parental care for *S. cinctus* is negligible compared to the egg-guarding component; however, in the laboratory, LF has observed female *S. cinctus* feeding in the nest. If female feeding in the nest also occurs in the field, it would decrease the cost of provisioning even further. Moreover, it is reasonable for species that provision seeds that are very small relative to the size of the female to incur minimal cost, but we suspect the cost is greater for *P. japonensis*. Particularly when several drupes are attached to a single stem and are all dragged back to the nest together, the energy required for *P. japonensis* females to transport such a load relative to body size over a distance as great as 15 m is likely to be considerable. Although constrained by semelparity, which precludes the cost to future reproductive success, there is likely a cost in terms of the number/size of fertile eggs produced.

Another important trait for which variation exists between members of this provisioning cluster distinguishes the Japanese members from their single North American peer. *Sehirus cinctus* is the only member of the provisioning club that does not also produce trophic eggs. LF has verified this with both *S. cinctus cinctus* and *S. c. albonotatus.* Trophic egg production is essential to the success of *P. japonensis* and *A. rotundus* offspring. The very poor quality of the available drupes experienced by *P. japonensis* means that mothers often cannot find acceptable drupes in a timely fashion to provision the nest, and trophic eggs would mitigate the risk of starvation and cannibalism until acceptable drupes are provided (Filippi et al. 2002; Hironaka et al. 2005). In the laboratory, first instar *C. niveimarginatus* could not penetrate intact *Thesium chinense* seeds, but they could successfully feed on the endosperm when the tough outer drupe coat was removed. Post-hatch trophic eggs sustain nymphs until they reach the second stadium and can penetrate and feed on the seeds (Baba et al. 2011). Both *A. triguttulus* and *P. japonensis* have been shown to increase the ratio of trophic eggs produced per viable egg under resource-constrained conditions (Kudo and Nakahira 2005; Filippi et al. 2012). Moreover, resource availability affected the impact of trophic egg feeding on *A. triguttulus*; nymphs developed faster when allowed to feed on trophic eggs in the presence of abundant resource, but survivorship was not affected. However, when deprived of trophic eggs under resource-limited conditions, survivorship was severely reduced. In fact, nymphs failed to molt to the second stadium (Kudo and Nakahira 2004). Interestingly, the rate of cannibalism (nymphal feeding on viable eggs) did not appear to be impacted by access to trophic eggs. Moreover, it is curious that cannibalism has not been observed in *S. cinctus*, the only species in this group that does not produce trophic eggs. Thus, resource constraints in terms of abundance and ability of the young to access the nutritional component of the resource and mitigation of cannibalism appear to have been the main factors promoting the evolution of trophic egg production in the other species.

8.3 Future Directions

8.3.1 Describing the Sister Species

Clearly there is much need for comparative studies that manipulate the ecological conditions of the members of this parental club, but with regard to *Parastrachia* research, where do we go from here? Detailed studies on the behavior of the sister species alluded to in Chap. 1 are certainly called for, but unfortunately, the species remains elusive. SN searched in likely areas of Laos and Vietnam, two countries within the reported range of *P. nagaensis;* however, both trips were unsuccessful. We continue to hope that we will find it one day and be able to clarify the resource, ecological constraints, and behaviors of this shy sister.

8.3.2 Ecological Cues, Suppression of Metabolic Rate, and Physiological Innovations Using Bacterial Symbionts

No work has been done to identify the ecological cues used by *P. japonensis* to regulate the number of individuals that become reproductively active each spring, while the remaining individuals continue their prolonged reproductive diapause without feeding until the following spring (Chap. 2). Is it the winter temperatures, which might also affect the productivity of the host tree? Or is it determined even prior to hibernation based on some condition experienced during development of the nymphs before they become adults? And, to be sure, there are more secrets that await discovery regarding the remarkable physiological adaptations that allow of *P. japonensis* adults to survive for 2 years without feeding, such as nitrogen recycling, which is dependent on a symbiotic bacterium. The curious timing of vertical transfer of the bacterial symbiont to eggs that is also seen in *Brachypelta atterima* (Cydnidae) requires clarification. Why do all the other parental cydnids secrete the symbiont together with the adhesive coating at the time of oviposition, yet *P. japonensis* (Hosokawa et al. 2013) and *B. atterima* (Schorr 1957) only do so just prior to hatch? Studies on the roles and functions of the bacterial symbionts continue to shed light on the intimate relationship *P. japonensis* has with its gut microbiota and their evolutionary history.

Of course, the fascinating gregarious nature of *P. japonensis* warrants further scrutiny and is the subject Tojo Sensei was investigating just prior to his death. What factors determine the size of the aggregations, which range from just a few individuals to thousands. Humidity did not appear to be a major factor, but this should be explored again.

8.3.3 Lingering Questions About Mating Behavior

Questions about mating behavior remain unresolved, as well (Chap. 3). What is the function of the male thrusting behavior? Time-lapse freezing of pairs in copula might clarify that and would allow visualization of the sperm on its path to the spermatheca. It would also be fascinating to verify whether any kind of sperm precedence pattern is at play here or even whether multiple males fertilize a female’s brood.

8.3.4 Regulation of Trophic Egg Production

Future studies on trophic egg production (Chap. 4) to determine whether the timing of oviposition is genetically predisposed or facultative are needed. It would also be of great interest to determine the cues that females use to assess resource abundance. Are they assessing abundance while they feed on the host tree to produce eggs and simultaneously assessing competition level based on how many drupes had already been fed on by other females?

8.3.5 Parent-Offspring Conflict and Sibling Rivalry

In addition to assessing the relative and absolute costs of guarding, progressive provisioning, and trophic egg production, there is a need for further studies on parent/offspring communication and conflict. Moreover, in this semelparous species with no opportunity for future reproductive success, there is much potential for intra-brood sibling conflict. The earliest instars start off at very similar weights, largely due to synchronized hatching (Chap. 5). They then feed cooperatively, aggregating on the drupe, completely covering it, because injecting the digestive enzyme into the drupe together facilitates feeding. This cooperative feeding results in fairly similar weight gains among the first and second instar nymphs. However, as the nymphs mature, the feeding pattern gradually transitions to competitive, and weight disparity among nymphs becomes apparent. Sibling conflict from this perspective requires further investigation.

We also know that mothers communicate with their offspring using vibrational stimuli, but research on potential begging cues by offspring is lacking. While volatile chemicals might be effective begging cues when multiple broods are involved, we anticipate that more individual cues are used with intra-brood sibling conflict in semelparous species such as *P. japonensis.* Future investigations are needed to identify the cues used by *P. japonensis* nymphs in sibling rivalry.

8.3.6 Navigating at Night

Navigation has not been explored extensively in the cydnids, but it seems likely that it is much more developed in *P. japonensis*, which must navigate great distances and tortuous paths between the nest and the food source than the cydnid progressive provisioners which nest among the seeds that they provision. Much has been discovered about how *P. japonensis* navigates while provisioning (Chap. 6), but many questions remain. Future investigations could focus on the criteria females use to choose a canopy gap to navigate by. While celestial cues are stable and the changes through the night predictable, canopy gaps will vary with even a breeze. It is curious that females rely on this fickle cue to provision at night.

8.3.7 Mitigation of Sibling Cannibalism

While cannibalism by nymphs is regularly observed in the field, we rarely observe it in the nest. It is likely that females suppress cannibalism when they are in the nest, however the female is often absent from the nest. What then keeps the young from eating each other while their mother is out searching for dinner? We carried out a preliminary study in an attempt to sort this out (unpublished data; Filippi et al. 2009).

In the laboratory, we established five different nest conditions in lidded clear plastic rearing cups (~10 cm diameter, 4 cm height). Nests contained soil, leaf litter, and five nymphs, and five to seven cups were prepared for each of the five conditions. Because we were trying to ascertain how cannibalism is mitigated when the female is out foraging, the mother was removed from all nest cups. The conditions of the nests varied with regard to nymph relatedness and substrate familiarity (Fig. 8.2a). Every nest in the group ($n = 5$) where all nymphs were unrelated and the substrate was foreign (Group E) showed evidence of cannibalism by 24 h (Fig. 8.2b). On the other hand, just 1/7 (14.3%) nests in the group of siblings only in their original substrate showed evidence of cannibalism by 24 h. When substrate was foreign but the nymphs were all siblings (Group B), this percentage increased to 29%. However, in the group with the original substrate, but one stranger among the siblings (Group C), the percentage of cannibalized nests jumped to 85.7%! This was a higher percentage than the group with one stranger and unfamiliar substrate (Group D; 57.4%). Interestingly, we found that in the nests that were cannibalized, a sibling was just as likely to be the victim as a stranger (Fig. 8.2c). By 10 days without food or mother, cannibalism increased in all groups, but was more than twice as prevalent in the two groups with unrelated nymphs than in the group with all sibs and original substrate (Fig. 8.2d). The finding that fewer nests in the group with both one foreign individual and foreign substrate had lower cannibalism than the group with only one foreign individual but original substrate is puzzling. However, the results suggest that in the presence of chemical cues from siblings and the original nest substrate cannibalism is suppressed, but nymphs are released from suppression and are free to cannibalize once the chemical cues are unfamiliar. This is reasonable as the only time nymphs should experience unfamiliar chemical cues in nature is after they become independent and relocate to the foraging area with thousands of unrelated nymphs. This study needs to be repeated with a larger sample size and expanded to verify specific factors in the nest that might serve as chemical cues. A likely target might be the liquid waste excreted by the female that is apparently used in homing (Chap. 6).

We anticipate that further investigation and comparison of the ecological parameters that have led to the evolution of complex parental care behaviors in *P. japonensis* and the provisioning cydnids will continue to contribute valuable information to our understanding of the selective pressures that lead to the evolution of parental care and strengthen the value of this exclusive parental club as a model system in parental care research.

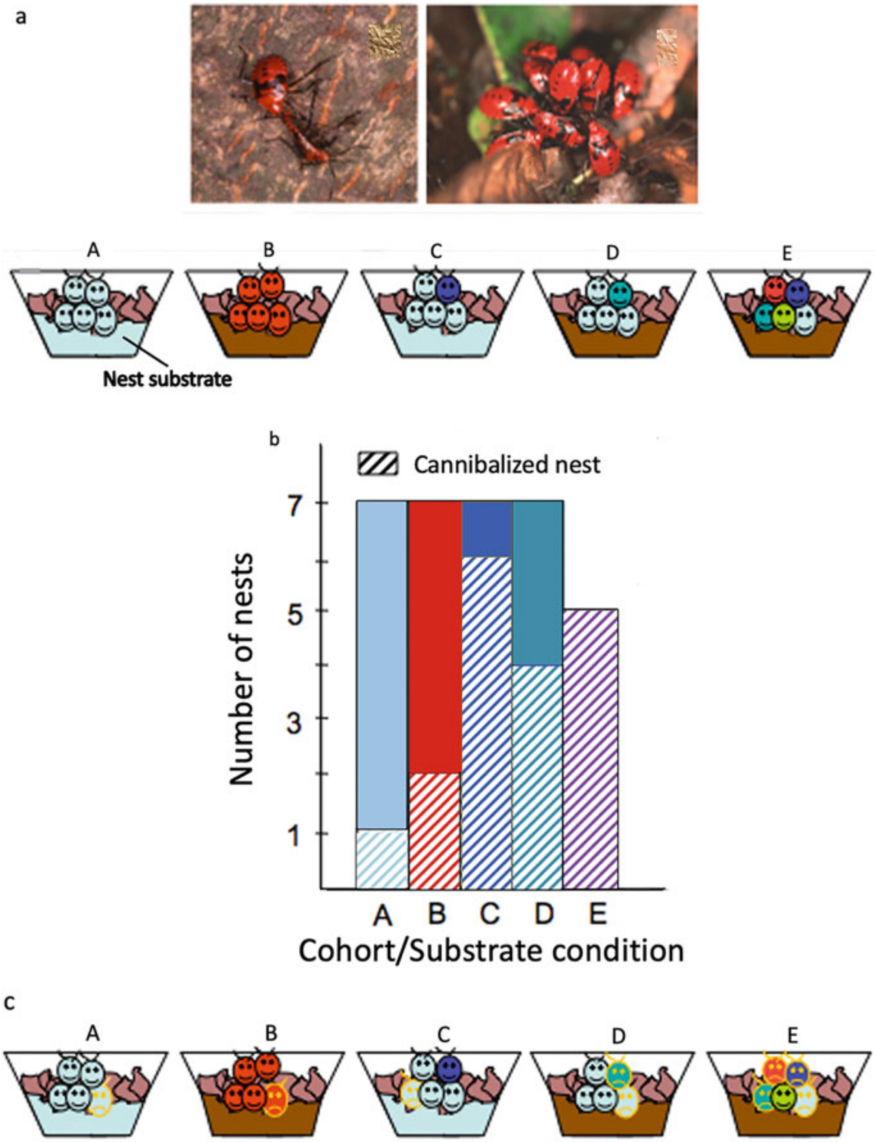

Fig. 8.2 The impact of chemical cues on sibling cannibalism. (**a**) Upper, fifth instars cannibalizing another fifth instar in isolation (left) and in aggregation (right). Lower, third instar nymphs were exposed to different nesting conditions, as indicated by the color of the nymphs and substrate: (A) all siblings in original nest substrate; (B) all siblings in “other nest” substrate; (C) four siblings and one stranger in original siblings’ nest substrate; (D) four siblings and one stranger in stranger nest substrate; (E) five unrelated nymphs in strange nest substrate; different color nymph is the stranger. (**b**) Number of nests that had evidence of cannibalism at 24 h. *, Fisher’s exact Test, 2 × 5 contingency, $p = 0.008$. (**c**) Target of cannibalism indicated by yellow outline on nymph. (**d**) Percent of nests in each group that had been cannibalized over 10 days in the absence of food and mother. (Unpublished data; conference abstract, Filippi and Nomakuchi 2009)

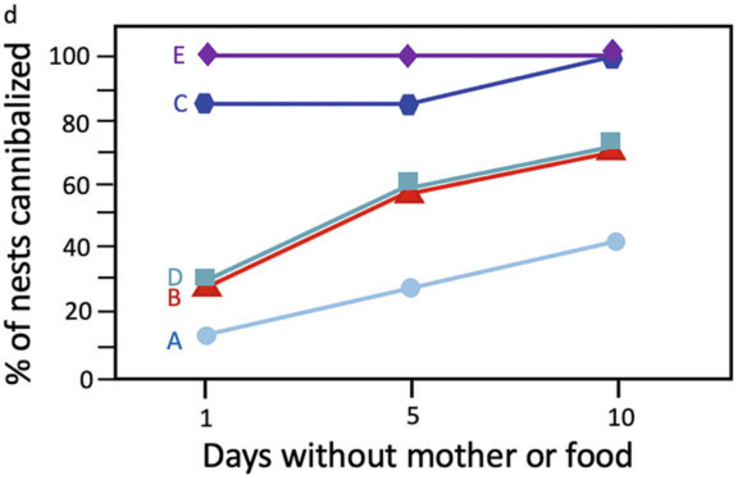

Fig. 8.2 (continued)

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