# Chapter 5
# Parent-Offspring Communication

**Hiromi Mukai and Shintaro Nomakuchi**

**Abstract** Parent-offspring communication is an indispensable capability for many social insect species that allows them to make full use of elaborate and complex parental care activities. *Parastrachia japonensis* Scott (Hemiptera: Parastrachiidae) is one such species. This chapter explains two astonishing phenomena, brilliant examples of parent-offspring communication via vibration that were recently discovered in this species. The first half of the chapter delves into parent-embryo communication that regulates the timing of egg hatching. Parent-embryo communication ensures synchronized hatch and mitigates sibling cannibalism. The second half of the chapter explores parent-nymph communication that involves a mother calling nymphs to gather on the drupes that she brings back to the nest. Parent-nymph communication ensures that nymphs gain equal access to food and likely keeps them hidden from predators until the mother returns to the nest. These communication behaviors are discussed from the viewpoint of fitness of both parents and offspring.

**Keywords** Hatching · Provisioning · Prenatal and postnatal parent-offspring communication · Substrate-borne vibration · Synchronization

## 5.1 Introduction

Parent-offspring communication involves transmission and processing of information about physiological and/or ecological conditions or requirements from parent to offspring or from offspring to parent. It appears that in subsocial insects, including *Parastrachia japonensis* Scott (Hemiptera: Parastrachiidae), parent-offspring

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communication often plays an important role throughout the process of all parental care behaviors in the family (Cocroft and Hamel 2010; Costa 2006). For example, nymphs of a subsocial treehopper clustered on a tree branch call their mother via substrate vibration for defense against an approaching enemy; the mother then approaches the enemy and threatens it, even if there is risk to her own survival, leading not only to increased fitness for the nymphs but also for the mother (Cocroft 1999). Substrate vibration from nymphs induces defensive behavior by the mother in this case. Moreover, larvae of subsocial burying beetles physically touch the parents' head with their legs on a carcass ball in a nest chamber when the larvae want food. In response to this larval begging, parents feed the larvae by regurgitation (Rauter and Moore 1999; Smiseth and Moore 2004). In this study, physical contact from the larvae induced feeding behavior by parents. These examples demonstrate that parent-offspring communication is likely to be essential for all interactions between parents and offspring in the process of parental care activities to ensure that all care behaviors are carried out successfully, e.g., defense against predators and feeding.

The studies discussed above exemplify the case where offspring are the signalers and parents are the receivers; however, examples where the parents or other siblings are the signalers and offspring are the receivers are also known. For example, it has been reported that hatchlings of the burying beetle direct their movement toward the sound that a parent makes in the nest (Costa 2006) and that, in order to maintain group cohesiveness, family members of treehoppers (Cocroft 2005) and sawflies (Fletcher 2007) recruit other family members to a new feeding site using substrate-borne vibration. However, to the best of our knowledge, there is no report demonstrating that a parent of another subsocial insect repeatedly uses vibration signals to communicate with offspring each time it progressively provisions the nest.

Can we identify any specific conditions that might shed light on why parent-offspring communication has evolved in subsocial insects, particularly communication that serves as an interaction tool for care behaviors between parent and offspring and not in insects whose parents do not engage in post-ovipositional care of offspring? There are probably at least two conditional factors that could have promoted the evolution of parent-offspring communication in subsocial insects.

The first factor relates to a basic condition of the physical parent-offspring relationship. One of the most obvious features that the emergence of post-ovipositional parental care has brought to the insect is the very state that parents and offspring remain together at a specific site, e.g., a nest, for a period of time. For example, in many insect species with guarding behavior of eggs and/or post-hatched offspring by parents, the parents and offspring remain together continuously even after oviposition has completed. This inevitability of cohabitation could have led to the occurrence of "family" in subsocial insects. Because family members would have interactions among themselves, approaching or contacting each other, especially during various types of intra-familial actions operating through parental care or sibling competition, they would have been able to use various kinds of stimuli or displays functionally working through short distances as signals to inform other family members about their own condition or requirements or to determine the same type of information from them. Even low-cost, weak stimuli that can only be transmitted in an isolated and small nest would have been enough to use as functional signals in a family. The lower cost of the transmission of information would have favored the evolution of intra-familial communication.

The second factor stems from theories of the evolution of animal communication. Communication is the system that involves transmission of any information between signalers and receivers. Because signals are actions or structures that signalers display to manipulate the receivers, they are considered to co-evolve with the response of the receivers: the signals evolve toward improved effectiveness in manipulation of the receivers, and the response of the receiver evolves against the improved manipulation by the signalers. In this way the signals continue to evolve to be ever more effective against antagonistic responses by receivers, etc., instead of evolving for simple improvement in the effectiveness of information transmission (Davies et al. 2012). Therefore, signals must include honest information on average because dishonest signals are costly to the receivers. Receivers would abandon utilization of dishonest signals, and, ultimately, the signal-receiving system would be eliminated. Behavioral ecologists have discussed several necessary conditions that must be met for signals to be kept honest, including index, handicap, and common interest (Davies et al. 2012). In the evolution of parent-offspring communication in subsocial insects like *P. japonensis*, what condition might have been most important for signals to remain honest? It could be the common interest between parent and offspring through their kinship. Because family members have a kinship with each other, selfish signals of one member in the family would be accepted by the other members in the family as long as direct or indirect fitness of the receivers increases.

In this chapter, we will first explain how *P. japonensis* mothers communicate with embryos to synchronize hatch (Sect. 5.2) and then how they communicate with post-hatched offspring during provisioning behavior to synchronize nymphal feeding (Sect. 5.3). We will also discuss how these types of communication enhance offspring success.

## 5.2 Parent-Embryo Communication

### *5.2.1 Maternal Substrate Vibrations as Cues of Exquisite Synchronous Hatching*

Embryos of most animals develop while being protected by a capsule such as an eggshell. In contrast to more developed stages, generally embryos and newly hatched young are vulnerable to dangerous and changeable environments (Warkentin 2011a). Particularly during hatching, when embryos emerge from their egg capsules, simultaneous changes in the physical environment and their development status, as well as their biotic interactions, present the highest risks for feeble embryos. Therefore, hatching at a suitable timing is a vital survival strategy.

Animal parents of several species use a particular type of care during the hatching moment, i.e., "hatching care," to increase their offspring's chances of survival. For instance, some avian parents actively assist their offspring in emerging from a hard shell at hatching. Parents gently peck the shell with their bills immediately before hatching to facilitate the emergence of the chick (Tremaine 1974; Birmelin and Wolter 1986; Newton 1986; Bond et al. 1988). Just before hatching, chicks chirp from inside their eggs, and this sound causes parental hatching assistance behavior. It is strongly predicted that such a close parent-embryo relationship while hatching has led to the evolution of special signals and communication systems (called "parent-embryo communication"); however, studies on static embryos have scarcely been advanced.

This section introduces the interaction and communication between the parent and embryo during hatching in the subsocial shield bug, *Parastrachia japonensis* (Heteroptera: Parastrachiidae), discovered by our research group (Mukai et al. 2014). As described in Chap. 4, *P. japonensis* mothers show complex maternal cares that aid nymphs after hatching, such as production of trophic eggs, protection of nymphs, and progressive provisioning (Tachikawa and Schaefer 1985; Tsukamoto and Tojo 1992; Filippi et al. 2001; Hironaka et al. 2005). There have been many reports on the maternal care of *P. japonensis* for the "active" nymphs after hatching; however, there have been few reports on care of "static" embryos. To explore this topic, we undertook a study to answer the following questions:

Do female *P. japonensis* care for embryos before or at the moment of hatching?

If so, what kind of parental care for hatching does the female show?

## Exquisite Synchronous Hatching

The female *P. japonensis* weaves its proboscis through the interstices of the egg mass and attaches the proboscis to the eggs with saliva. Thus, the egg mass is protected by suspending it between the long legs of the female, such that the eggs are kept elevated without sticking to the ground. This is thought to have the effect of preventing predators such as ants from approaching the egg mass from the soil surface and protecting from insecticidal pathogens (Fig. 5.1).

The eggs have a whitish cream color immediately after being laid (Fig. 5.2a), but they gradually become pale pink over 10 days. Hatching begins soon after the eye spots become visible and nearly all eggs have turned red (Fig. 5.2b).

The hatching of the *P. japonensis* egg mass occurs synchronously. Hosokawa et al. (2012) reported that mothers of *P. japonensis* start to excrete a copious amount of symbiont-containing white mucus from the anus onto the egg mass at around 40 min before egg hatching (median 39 min; range 30–50 min; $n = 10$). After the excretion behavior, the mothers lifted the egg mass using the proboscis and resumed the egg-guarding posture (Fig. 5.3a). Then, after a while, the nymphs broke the eggshells all at once and began to hatch. By 10 min after the start of hatching, 90.3 ± 7.3% (mean ± SD) of the embryos had emerged from their shells (Fig. 5.3b). Newly hatched nymphs remained motionless for a few minutes and then gradually

**Fig. 5.1** Egg-guarding female *P. japonensis*. Females hold the egg mass in the nest, suspended on the stylets, lifted off the ground. Photo credit, Mantaro Hironaka

**Fig. 5.2** Female *P. japonensis* guarding egg mass. The eggs are (**a**) whitish cream color immediately after being laid, and (**b**) fertile eggs turn pink with visible eyespots just before hatching

began to move (Fig. 5.3c). They started to walk around actively and aggregated on the egg mass within 5 min (Fig. 5.3d). The newly hatched nymphs immediately took up the mucus secretion and the trophic eggs with their respective proboscises (Fig. 5.3e). Interestingly, it was found that similar batch hatching was not observed when the egg mass that had been smeared with symbiotic bacteria was separated from the female parent (Fig. 5.3f-j). In such egg masses, hatching occurred bit by bit after the first individual started to hatch. After 30 min from the end of excretion, about half of the individuals in the egg mass remained in the shell.

This suggested that the symbiont-containing mucus secretion did not affect the timing of hatching and that female involvement after mucus secretion was most likely occurring to induce synchronous hatching.

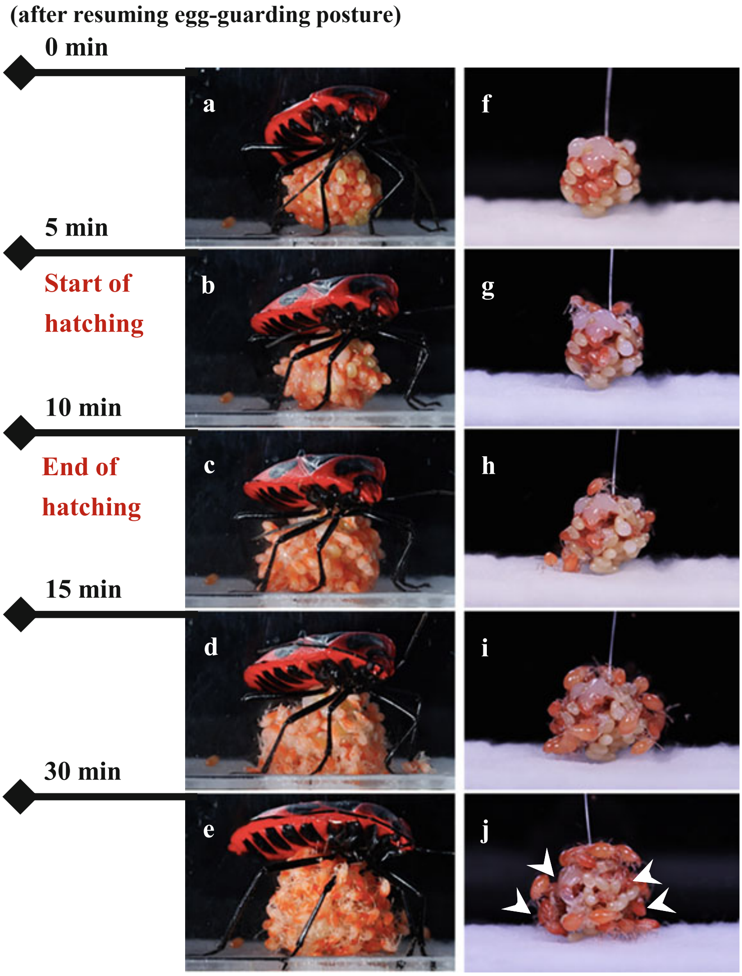

**Fig. 5.3** The hatching processes of control (**a**–**e**) and mother-removed egg mass (**f**–**j**). Arrowheads indicate nymphs that are still hatching or which remain in the eggshell (**j**). Whitish eggs are trophic eggs. Adapted from Mukai et al. (2014)

### Vibrating Behavior by Mothers

We hypothesized that the synchronous hatching in *P. japonensis* was related to the female's behavior at the moment of hatching. To monitor maternal behavior, we observed seven mothers holding a mature egg mass, which turned pink and which developed conspicuous eye spots immediately before hatching. And it was then that we discovered the unique maternal "vibrating behavior."

The video monitoring observation revealed that all mothers showed a physical vibration at the time of nymphal hatching. Mothers vibrated on their suspended egg

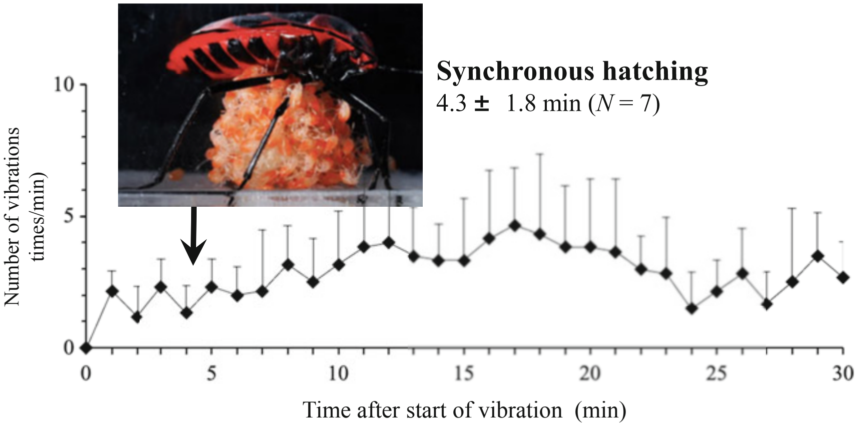

**Fig. 5.4** Maternal vibration at the moment of hatching. Black arrow indicates the initiation of synchronous hatching. $n = 7$. Error bars represent SD. Adapted from Mukai et al. (2014)

mass while maintaining the egg-guarding posture. Mothers showed intermittent faint vibrating behavior, i.e., they did not move for several tens of seconds after the prior vibration; then they vibrated their body only once. Figure 5.4 shows the occurrence pattern of maternal vibration. Means + SD are shown for numbers of vibration/min from the start of vibration generated by seven mothers, and at the time indicated by a black arrow, the synchronous hatching began suddenly.

Observation using high-speed photography revealed that maternal vibration comprised only a faint single vertical motion, moving the abdomen slightly, just 2–3 mm vertically up and down. The single vertical motion took approximately 0.3 s to move the mother's abdomen. To quantify the temporal pattern of the maternal vibration, we counted the abdominal movements per minute for 30 min from the beginning of the vibrating behavior (Fig. 5.4). Mothers vibrated, on average, a total of 87.5 ± 1.8 times (mean ± SD), constituting 2.9 ± 1.8 times per minute of vibration during this period. Although no distinct peak of the maternal vibration or remarkable change of the mother's behavior was observed, highly synchronous hatching began at 4.3 ± 1.8 min (Fig. 5.4) after the start of vibration. Some mothers continued the vibrating behavior for more than 6 h.

### 5.2.2 *Effect of Maternal Vibration on Hatching Pattern*

Does the maternal vibration affect hatching pattern?

To verify whether the maternal vibration served to synchronize hatching, we monitored the temporal pattern of hatching of eggs assigned to one of four groups: control (with mother) group, mother-removed group, and two artificial vibration groups.

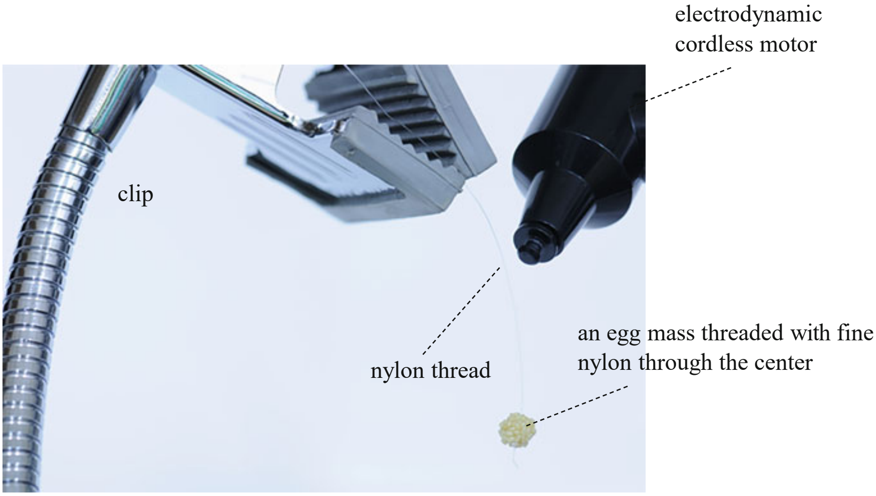

**Fig. 5.5** Experimental design of artificial vibration

The vibration of the female parent was reproduced using a cordless motor (Fig. 5.5). In the mother-removed group and two artificial vibration groups, we isolated mature egg masses from mothers immediately after they finished the excretion behavior. Then we weaved a fine nylon thread through the midline of each egg mass and artificially suspended it by holding it with a clip. For the artificial vibration, we used two different vibration patterns: intermittent artificial vibration and continuous artificial vibration. For the intermittent vibration group, we provided artificial vibration using a cordless motor during 15 min from the end of mucus excretion. We switched the motor on for an instant every 30 s with the cordless motor attached to the end of the nylon thread. For the continuous vibration group, we provided continuous artificial vibration for 15 min from the end of excretion.

The results clearly revealed that when we exposed the egg masses to intermittent artificial vibration, the embryos began to hatch rapidly one after another during approximately 5 min after the start of vibration. The average percentage of hatched eggs ± SD was 77.6 ± 11.8% within the first 30 min, which was a similar level to the control group (90.3 ± 7.3%). However, when the mothers were removed from the egg mass, the pattern of hatching changed drastically. In the mother-removed group, about half of the embryos failed to hatch, and the other half hatched asynchronously. Embryos took a long time to hatch, with only 5.0 ± 4.5% of the embryos hatching within the first 30 min (Fig. 5.6). Interestingly, when we exposed egg masses to continuous artificial vibration, the embryos also took a long time to hatch, with only 14.9 ± 13.4% of the embryos hatching within the first 30 min (Fig. 5.6). The embryos that had not hatched during the observation never hatched thereafter; all blackened and died. These results suggest that the embryos sense whether the female parent is vibrating or not and respond by synchronizing the timing of their hatching.

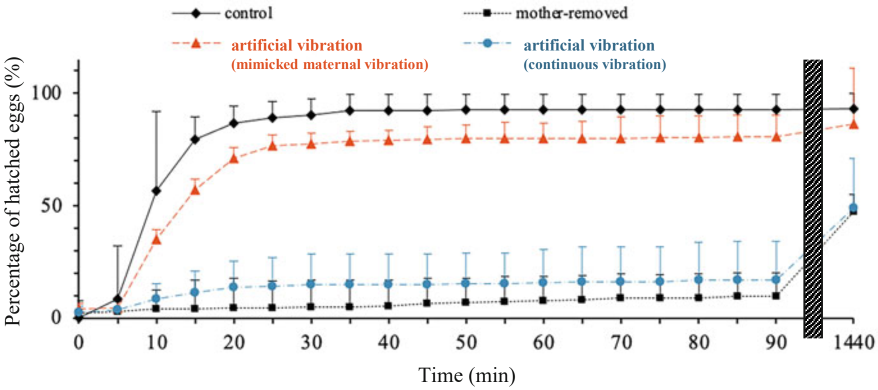

**Fig. 5.6** Hatching pattern of embryos exposed to the different treatments. Means + SD are shown for the percentage of hatched eggs at 5 min intervals for the first 90 min and for 24 h from the start of hatching. Adapted from Mukai et al. (2014)

Embryos enclosed in the eggshells have a sophisticated mechanism for distinguishing maternal vibration.

### *5.2.3 Maternal Care as a Necessary Cue for Embryo Hatching*

Mukai et al. (2012) described the functions of hatching care as classifiable into two groups: “hatching assistance” and “hatching regulation.” Hatching assistance, a form of parental care performed by parents to provide some assistance for their young, enhances hatching success, as shown by parents of most avian species: they break into the hard eggshell to assist their young (Tremaine 1974; Birmelin and Wolter 1986; Newton 1986; Bond et al. 1988). Hatching regulation is a form of parental care that is performed by parents to provide some physical or chemical stimulation for embryos to regulate the hatching pattern, as seen in subsocial spiders: mothers adjust the egg-hatching time in response to the threat of predation (Li 2002). The hatching care of *P. japonensis* is evidently different from other examples of hatching assistance in avian, crocodilian, and arachnid species.

In *P. japonensis*, mothers give only a faint vibration to the egg mass. In fact, even when we provided continuous artificial vibration to the isolated egg mass that did not match the temporal pattern of maternal vibration, the hatching tended to fail and to occur asynchronously (Fig. 5.6). This observation revealed that it was not the actual physical vibration that induced shell rupture. However, we also found that when we provided continuous artificial vibration, embryo hatching was not only asynchronous but also some embryos failed to emerge from their shells. This suggests that the female *P. japonensis* vibrations in a particular pattern serve as a necessary cue for hatching.

Warkentin (2011a) classified hatching systems related to hatching cues into two groups: "spontaneous hatching (SH)" and "environmentally cued hatching (ECH)." "Fixed hatching" or "normal hatching" is synonymous with spontaneous hatching used in hatching studies of amphibians (Warkentin 2011b) and reptilians and avians (Ewert 1991). SH is defined as a hatching system that operates without an external cue (Warkentin 2011a; Gomez-Mestre et al. 2008; Saifur et al. 2010). SH occurs at a consistent stage in development or, potentially, after a consistent embryonic period, irrespective of environmental conditions. In contrast, ECH is defined as a "decision" based on information. It might depend on a specific behavioral or physiological process that is cued environmentally (Warkentin 2011a). For an animal species that depends entirely on an SH system, or on both SH and ECH, embryos hatch with no stimulation. In a species depending solely on ECH, hatching will not occur without the environmental cue. Embryos die when the energy reserves become exhausted. For example, in some solitary zooplankton *Daphnia* species, embryos never hatch without moisture stimulation (Arnott and Yan 2002). It is likely that the hatching system of *P. japonensis* is a type of ECH only. Therefore, interception of the maternal vibration or providing continuous artificial vibration might affect the hatching success.

In Mukai et al. (2014), the form of hatching care was redefined as below: "Hatching assistance" is a form of parental care by which parents assist hatching by reducing the physical burden of embryos. "Hatching regulation" is a form of parental care by which the parents regulate the temporal pattern of hatching without reducing the burden. We have classified the function of hatching care in accordance with ascertaining whether parental care examined in previous studies served (1) to improve the hatching success and (2) to influence the hatching pattern. Therefore, in addition to these indexes, we must incorporate consideration of a new index: (3) how parental care is related to embryo hatching. In this paper, we proposed and assessed a more appropriate definition and verification methods of functions related to hatching care than those reported in the literature (Mukai et al. 2012). Our proposals are expected to clarify previous and future studies of parental hatching care. Future studies are expected to extend the classification of hatching care and to elucidate the evolutionary background of hatching care and parent-embryo interactions.

### 5.2.4 Maternal Vibration and Synchronous Hatching in Closely Related Species

Closely related species to *P. japonensis* also have been found to display maternal vibration and synchronous hatching. Burrower bugs, *Adomerus rotundus* (Heteroptera: Cydnidae), exhibit maternal care including defense against predation and provision of food. We previously found that female *A. rotundus* also displayed

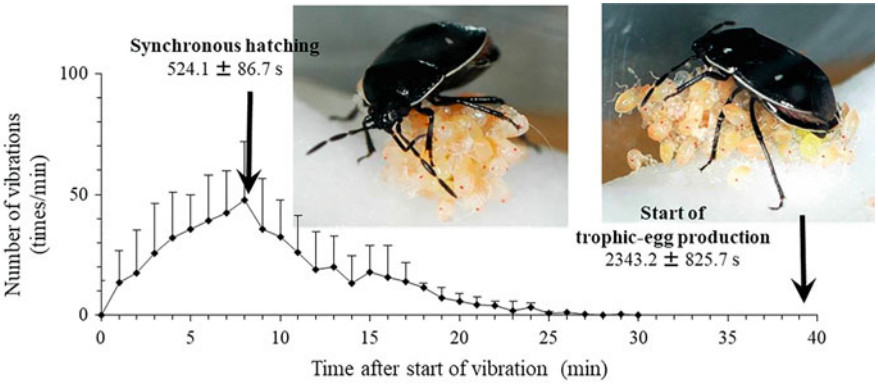

**Fig. 5.7** Maternal hatching vibration in *A. rotundus*. Black arrows indicate each event of maternal care. Adapted from Mukai et al. (2012)

physical vibration (shaking the body rhythmically) while maintaining the egg-guarding posture, i.e., holding the egg mass under the thorax between the forelegs and midlegs, and promote synchronous hatching (Mukai et al. 2012). However, although both the hatching care of *P. japonensis* and *A. rotundus* includes vibration of their egg masses, some important differences are apparent in the features of the vibrating behavior.

One notable difference is the occurrence pattern of the vibrating behavior. In *A. rotundus*, the maternal vibration increased initially over time, reaching a peak at approximately 9 min after the start of vibration, when most of the eggs hatched (Fig. 5.7). This vibrating behavior lasted about 23 min. However, in *P. japonensis*, the maternal vibration did not have a distinct peak. Rather, it gradually increased and then plateaued. Vibrating behavior of *P. japonensis* lasted interminably over 6 h from the beginning of vibration, even after almost all embryos' hatching had already finished (Fig. 5.4). Detailed temporal patterns of vibration were also different in these two species. In *A. rotundus*, maternal vibration apparently took place intermittently with alternate occurrence of two conspicuous periods: a vibration period and a pause period. The vibration period included several pulses, which comprised the single vertical motion of the vibrating mother's body. The vibration of the female *A. rotundus* was composed of intermittent pulse groups in the low-frequency region below 100 Hz. On the other hand, *P. japonensis* mothers provided a faint vibration to the suspended egg mass, i.e., mothers vibrated their bodies only once per several tens of seconds.

Among closely related species of some crabs, the mothers of which generate abdominal pumping at hatching, some comparisons have been made of the frequency and the occurrence pattern of maternal pumping behavior (De Vries et al. 1991; Christy 2011; De Vries and Forward Jr. 1991). The differences between the hatching care are presumably attributable to the physiological constraints of eggs, such as their respective sizes (De Vries and Forward Jr. 1991). Considering that, differences between *P. japonensis* and *A. rotundus* might be derived from

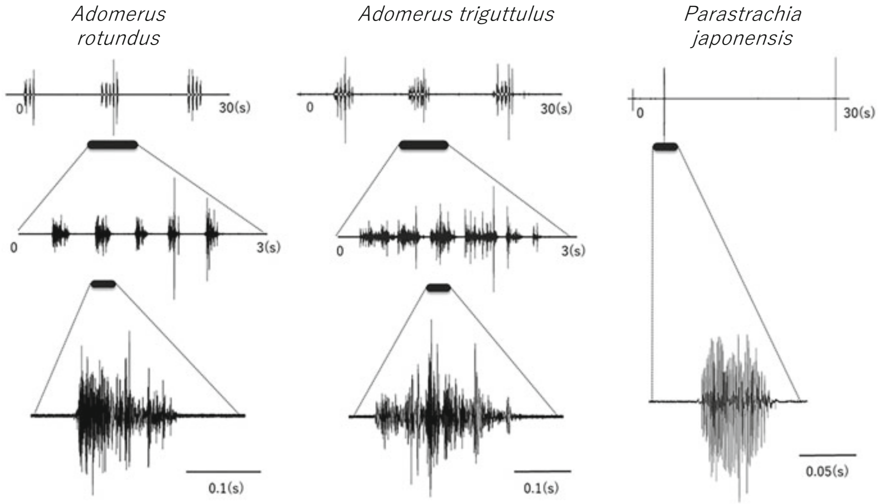

**Fig. 5.8** Time-based waveform of maternal hatching vibration in three species, *Adomerus rotundus*, *A. triguttulus*, and *Parastrachia japonensis*. Adapted in part from Mukai (2019)

physiological constraints. Some species of burrower bugs (Cydnidae: Sehirinae) also show maternal care, including egg guarding, production of trophic eggs, protection of nymphs, and progressive provisioning (*Sehirus cinctus*, Sites and McPherson 1982; *Adomerus triguttulus*, Nakahira 1994; *Canthophorus niveimarginatus*, Filippi et al. 2009; *Adomerus variegatus*, Mukai et al. 2010; *Adomerus rotundus*, Inadomi et al. 2014). Moreover, in some species of burrower bugs, maternal hatching vibration has also been observed. Measuring the vibration with a non-contact-type Laser Doppler Vibrometer revealed that *Adomerus triguttulus*, which has a similar life history to *A. rotundus*, shows a similar vibrational pattern to that of *A. rotundus* (Fig. 5.8). To elucidate the diversity of the stimulus in hatching care, future studies should examine more details of the physiological and ecological constraints of these species and other subsocial bugs practicing complex maternal care resembling that of *A. rotundus* and *P. japonensis* provided by mothers.

### 5.2.5 Adaptive Function of Maternal Care at the Moment of Hatching

Recent studies have also provided results that explain the adaptive significance of simultaneous hatching. Mukai et al. (2018) tested the hypothesis that synchronous hatching induced by maternal vibration in *A. rotundus* prevents sibling cannibalism. Mothers and their mature egg masses were allocated to three groups: synchronous hatching by maternal vibration (SHmv), synchronous hatching by artificial vibration

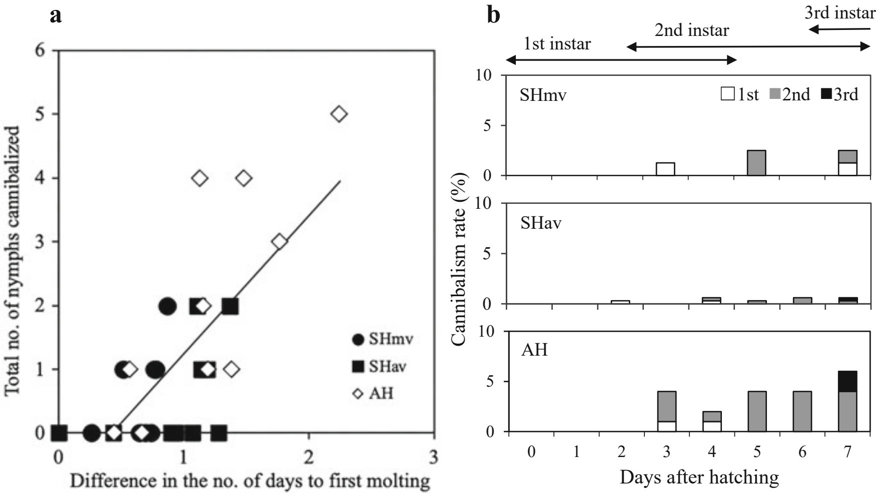

**Fig. 5.9** (**a**) Correlation between number of days to first molting and total number of *A. rotundus* nymphs cannibalized and (**b**) timing of sibling cannibalism within clutch. *SHmv* synchronous hatching by maternal vibration; *SHav* synchronous hatching by artificial vibration; *AH* asynchronous hatching. Adapted from Mukai et al. (2018)

(SHav), and asynchronous hatching (AH). Then they investigated the influence of each hatching strategy on the occurrence of sibling cannibalism of eggs and early instar nymphs in the laboratory. No difference in the proportion of eggs cannibalized was observed among the three groups. However, the proportion of nymphs cannibalized was higher in the AH group than in the SHmv group (Fig. 5.9, Mukai et al. 2018). The number of days to first molting within clutch was significantly higher in the AH group than in the SHmv group (Fig. 5.9a). After examining the timing of cannibalism, it was clear that cannibalism occurred with high frequency during the period of molting from the first instar to the second instar, and also from the second instar to the third instar (Fig. 5.9b). We sometimes observed early instar nymphs being eaten by late instar nymphs. However, we often observed that immediately after molting, late instar nymphs were at a high risk of being eaten by early instar nymphs (Fig. 5.10). Molting individuals have a thin integument and cannot escape or protect themselves from conspecific or interspecific predation (Dick et al. 1990; Soluk 1990), so they are considered to be an affordable and familiar food source for starving nymphs. Such within-clutch interactions caused by AH may have been an evolutionary driving force for the unique maternal hatching regulatory system and synchronous hatching in *A. rotundus*. Endo and Numata (2020) also revealed evidence supporting that synchronized hatching observed in the brown marmorated stink bug stimulated by vibratory cues (Endo et al. 2019) helps eggs to avoid being cannibalized by their earlier-hatched siblings. They also show that other stink bugs with no synchronized hatching have little or no risk of sibling egg cannibalism (Endo and Numata 2020). Sibling cannibalism and synchronized hatching are likely to be closely related.

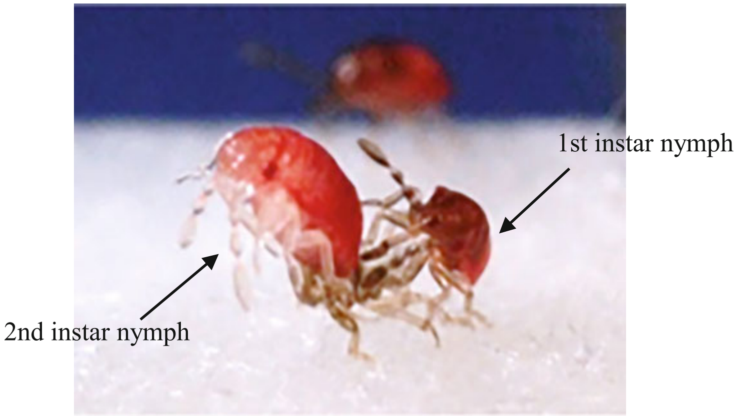

**Fig. 5.10** Sibling cannibalism of newly molted second instar by first instar nymph in *Adomerus rotundus*. Adapted from Mukai et al. (2018)

Synchronous hatching also could help the newly hatched nymphs form large aggregations more easily. Such aggregations might improve hatchling survival rates by effectively reducing the predation rate through cooperative defense (Henry 1972; Godfray et al. 1991), maintaining favorable conditions (Lauber and Darvas 2009), and/or obtaining food resources by group foraging (Way and Cammell 1970; Ralph 1976; Inoue 1986). In addition, synchronous hatching might function to keep the developmental stages synchronous, thereby enabling parents to provide care that is appropriate to the developmental stage of all or most nymphs at any given time. In several precocial avian species, some newly hatched chicks leave the nest after a few hours and start self-feeding under parental care. If the other eggs in the nest have not yet hatched at this point, then parents face the problem of whether to choose egg-guarding or offspring-protecting, which are two mutually exclusive behaviors. To avoid this dilemma, parents might synchronize hatching of chicks strategically, thereby eliminating the need for decision-making that would result in neglecting some offspring (Stoleson and Beissinger 1995). In any of these scenarios, some offspring would necessarily be neglected for part of the time. To give all offspring optimal care with optimal timing and to economize the duration of care, mothers might prompt eggs to hatch synchronously. It is also possible that synchronous hatching could increase the reproductive rate of the parents by shortening the parental care period.

In subsocial stink bugs, the nymphs often spend 10–15 days (third instar or fourth instar) under the protection of the female bugs. During this period, the nymphs live in dense aggregations of siblings in the nests and depend on trophic eggs and seeds of host plants supplied by the female parent for their food. In *P. japonensis*, synchronized hatching might also have other functions for hatched nymphs such as activating the taking up of the mucus secretion, which might be involved in uric acid recycling during the diapause period (Kashima et al. 2006; Hosokawa et al. 2010). Given these unique ecological peculiarities, in addition to the cannibalism avoidance described above, the influence of the parental care behavior of the female parent may be the background for the evolution of synchronous hatching. The acquisition of parent-embryo communication through vibration is an important means to achieve that synchronous hatching.

### *5.2.6 Conclusions About Parent-Embryo Communication in Subsocial Stinkbug*

Shield bugs and stink bugs specialize in vibration communication, and it is highly possible that they have acquired a communication system at the time of hatching by fully adapting the already existing vibration reception system (Cocroft and Rodriguez 2005; Čokl 2008). It is known that *P. japonensis* also has the vibrational receptors called "Femoral Chordotonal Organs (FCOs)" in all six legs (Nishino et al. 2016). In addition, it has been confirmed that just prior to hatching the embryos actively move inside the eggs. From these facts, it is considered that in *P. japonensis*, embryos immediately before hatching actively receive vibrational signals and construct bidirectional communication between parents and embryos. In future studies, we would like to clarify the process by which the evolution of the unique hatching communication system by the subsocial shield bug embryos occurred in the exposed biological environment.

## 5.3 Parent-Nymph Communication

Mothers of *P. japonensis* communicate with offspring at different stages of development. Although we have already explained about the communication between mothers and eggs, we have discovered that females also communicate with post-hatched nymphs when feeding them in the nest. Females emit a vibrational call after returning to the nest with a drupe; the nymphs then gather on the drupe. We designated this vibrational call "provisioning call." We will explain here how mothers emit the provisioning call to post-hatch nymphs and how nymphs respond to the call. Most of what we present in this section is based on the results about female "provisioning call" that were reported by Nomakuchi et al. (2012).

In this section, we first introduce a story about the discovery of the provisioning call, in addition to the behavioral conditions of a parent and nymphs when calling, and then we describe the vibrational characteristics of the provisioning call itself and, further, its functions. We consider that the provisioning call is one of the signals in the communication system between a signaling mother and receiving nymphs.

## *5.3.1 Provisioning Call*

### Discovery of the Provisioning Call

One of our research bases for this species, *P. japonensis*, was the Laboratory of Animal Behavioral Ecology, Department of Applied Biology, Faculty of Agriculture at Saga University, where a variety of intensive research in terms of parental care behavior, intra-familial conflict, and cooperation in this species has been carried out for a couple of decades. Although in the early stages of our research, most of our investigations were carried out in the field, we gradually moved to laboratory experiments to enable more controlled testing of various hypotheses about parental behavior. In most laboratory experiments, females (50–100 individuals) guarding their egg mass under leaf litter were collected together with their egg mass from our field site at Mt. Hinokuma, Kanzaki City, Saga, Japan, and were introduced into the laboratory in late May. Collected females and their egg masses were individually placed into transparent plastic cups (about 10 cm in diameter and about 5 cm in depth) filled with forest bed debris collected from around the actual nests in the field and kept in incubators under conditions of 25 °C and 14-h light/10-h dark. Using these females, several experiments have been carried out to observe parental behavior under laboratory conditions. Mantaro Hironaka, who had recently completed his doctoral dissertation on this bug, was the first to notice a faint buzzing sound when females returned to their nests laden with drupes. It was fortunate that he recognized the sound by chance while engaged in another procedure during a series of experiments unrelated to communication. This was just the moment when the "provisioning call" was discovered. The call was so low that it would never have been recognized in the field because of the background noise. It is considered that there are three fortunate conditions of the study that have contributed to discovery of the provisioning call. First, although the provisioning call could be a vibrational signal probably adapted to the physiological receiving capabilities of conspecifics, it also partially clearly involved audible airborne sounds that could be heard by a human. If it were only vibrational, we might never have recognized it. Second, our experimental observations were performed in the convenient environment of the laboratory under which sufficiently quiet conditions were possible instead of in the noisy field. Additionally, we could simply move our ears close to the cups containing a nest to hear the call. Third, the cups housing the nests were transparent so that observers could monitor the behaviors of females and nymphs from every direction when females were emitting the call.

## *5.3.2 When Do Females Emit the Call?*

In our investigation of the provisioning call, we first sought to determine exactly when females emitted the call, especially questioning whether the call was limited to

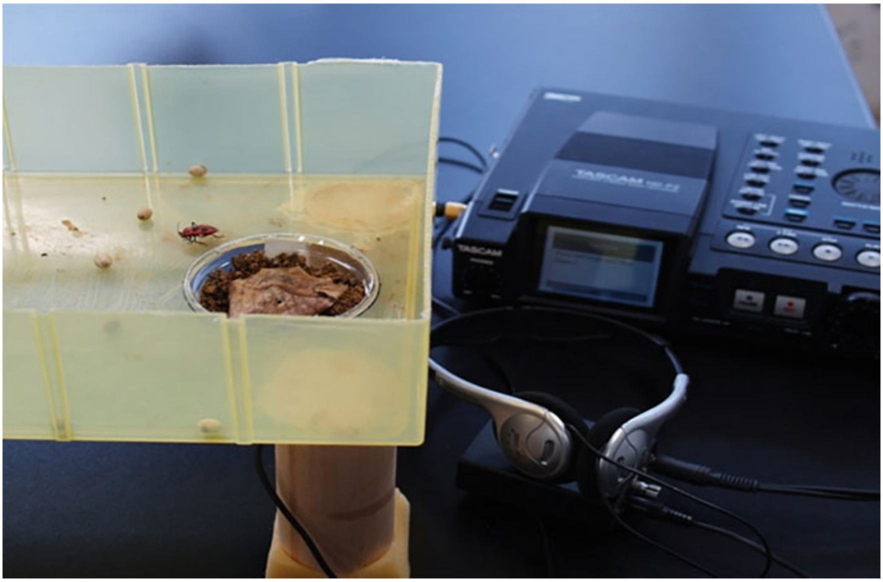

**Fig. 5.11** Observation table with a nest cup set into the bottom of the container/table and the digital recorder. Note the female foraging for drupes on the bottom of the container after leaving her nest

a particular time that coincided with any specific actions or behaviors by females and/or nymphs during parental care. The observation was carried out in the laboratory using a rectangular plastic container that was configured into a table (40 cm in length, 30 cm in width, 15 cm in height, with four legs, Fig. 5.11). A hole was cut into the bottom of the table where the nest cup could be set, such that the upper edge of the cup was flush with the bottom surface of the table where drupes that the females could collect were scattered, and the rest of the transparent nest cup protruded below the base of the container/table. In this way, the females could easily leave and return to the nest over the cup edge when foraging for a drupe, and activities inside the nest cup could also be easily monitored. Females that returned to a nest were continuously observed as long as possible. In other words, unless the female burrowed into the debris around the nest, we could observe her behaviors; simultaneously, all vibrations and/or sounds observed were also measured. All vibrational signals emitted through the cup wall were collected using a contact microphone (HOGA original contact microphone, TWA-3S, Kyoto City, Kyoto, Japan: http://www.hoga-kyoto.com/) attached to the outside of the bottom of the nest cup and were recorded on a digital sound recorder (TASCAM, HD-P2) with a 44.1 kHz sampling frequency (Fig. 5.11). Additionally, a condenser microphone (Audio-Technica, AT9842, Machida City, Tokyo, Japan) was set 2 cm above the nests to collect the airborne sound.

More than 100 females caring for nymphs were monitored according to the above procedure, and the sequence of behaviors that follows for one female was consistent for all females observed. Initially the call began to sound just when the female entered the nest cup, and it continued to be clearly heard, emitting from the direction of the female as she moved about in the nest. Observation of the female's body posture when the call was emitted revealed that the female was shaking her body while maintaining a narrow gap between the dorsal abdomen and wings, similar to the posture of calling crickets. These observations demonstrate that the call was definitely being emitted from the female. Further, we came to realize that that the call from the female was coordinated with a series of female behaviors during the process of provisioning the nymphs in the nest. The female began to call as soon as she entered the nest dragging the drupe that she had collected and continued to call intermittently in bouts inside of the nest while plowing her way through the nest debris, which included plant roots, organic soil, and rotten leaves. Upon encountering an aggregation of nymphs, the female placed the drupe next to the nymphs, but still kept it attached to her proboscis. The nymphs then began to approach and cling to the drupe that the female still covered with her body. When many nymphs had gathered and clung to the drupe, fully covering its surface, the female finally released the drupe from her proboscis and stopped calling. The female then moved about 2 cm away from the feeding nymphs and remained there for just a few minutes before departing the nest to collect the next drupe. Observations were terminated when the female left the nest, or at 10 min after the female dropped the drupe, even if she remained in the nest. This behavioral sequence was nearly identical in all cases that we observed ($n = 40$). Therefore, the provisioning call could be a necessary component of a programmed behavioral sequence comprising all the provisioning actions. In fact, we assumed that the call would serve as a special signal that females use to call the nymphs in the nest so they could easily and quickly encounter the food brought into the nest.

Further, we discovered that the call collected by the contact microphone on each observation of a female consisted of multiple sound bouts with various sound lengths. The length of all sound bouts and their gaps were recorded from actual hearing of the call with a headphone. The duration of each call was measured from start to finish with a stopwatch for individual females. Table 5.1 shows the results of four collected variables: the total number of sound bouts, the longest bout length, the percentages of short sound bouts (<2 s), and the total length of all sound bouts through an individual call for two nymphal stadia, the first and the third (Nomakuchi et al. 2012). The number of sound bouts was significantly larger, and the total length

**Table 5.1** Pattern of sound bouts in a provisioning call through nymphal growth (the first and the third stadia). Adapted from Nomakuchi et al. (2012)

| N | No. bouts | Longest bout length (min) | % Short bouts | Total length of bouts (min) |
|---|---|---|---|---|
| 1st 17 | 55.8 ± 4.1 | 1.12 ± 0.33 | 56.5 ± 3.5 | 36.16 ± 3.53 |
| 3rd 13 | 26.2 ± 4.6 | 2.17 ± 0.46 | 55.7 ± 4.6 | 12.90 ± 2.17 |
| *U* | 353.0 | 226.0 | 265.5 | 356.0 |
| *P* | 0.0002 | 0.1215 | 0.9499 | 0.0001 |

of all bouts was significantly longer, during the first instar than the third instar. There was no significant difference in the length of the longest sound bout between the first and the third instars. Furthermore, there was also no significant difference in the percentage of short sound bouts between the first and the third instars. The fact that the number of sound bouts and the total length of all sound bouts decreased possibly resulted in a shortening of the entire provisioning call with the progression of nymphal development. If the provisioning call functions to gather nymphs to the drupe that the females were trying to provide them, the present results are reasonable because older nymphs with better maneuverability should be able to approach the drupe more easily and quickly on their own.

### 5.3.3 Vibrational Characteristics of the Provisioning Call

We further tried to investigate vibrational characteristics of the provisioning call using the sound data that we had recorded. We had collected and recorded the call through the wall of the plastic nest cup to examine how females emit the provisioning call and how the call is associated with behavior of females and/or nymphs through observations in the laboratory. However, we realized that the wave quality of the call might have been transformed into a biased one when passing through the plastic wall. Therefore, we felt strongly that we should measure the call again by a more appropriate method, one that involved less wave transformation, so that we would be able to analyze its vibrational properties more appropriately. Thus, we decided to collect the call again from wild females more directly, under natural field conditions and without the plastic cup.

On a fine day with almost no wind at our field site at Mt. Hinokuma, three nests with third instars were chosen to collect the calls for analysis of their vibrational properties. Once we located a nest in the field, we gently inserted the short arm of an L-shaped iron clamp into the soil just under the nest, and the other arm of the clamp, sticking out, from the ground was attached to the contact microphone. We considered that the metal clamp would work as an extended probe for the contact microphone. We collected all vibrational pulses emitted from the nest when females returned with a drupe. Furthermore, to identify all background noises, we also collected the noise when females were absent from their nest. All vibrational pulses were recorded on a digital sound recorder, and data were input into a personal computer and analyzed with fast Fourier transform (FFT) analysis using the bio-acoustic analyzing software, Avisoft SASLab Pro (Berlin, Germany).

Although the provisioning call sounded just like a weak buzzing or fluttering sound, composed of a set of alternately repeating intermittent sound parts (sound bouts) and gaps (silent intervals) to the human ear, the vibrational properties of a segment of a provisioning call collected by the contact microphone in the field are shown in Fig. 5.12. Figure 5.12a indicates a waveform of the segment of the provisioning call by a female that was calling in her nest. The call clearly consists of repetitive clusters (bouts) of waves with varying range and amplitude. Some bouts

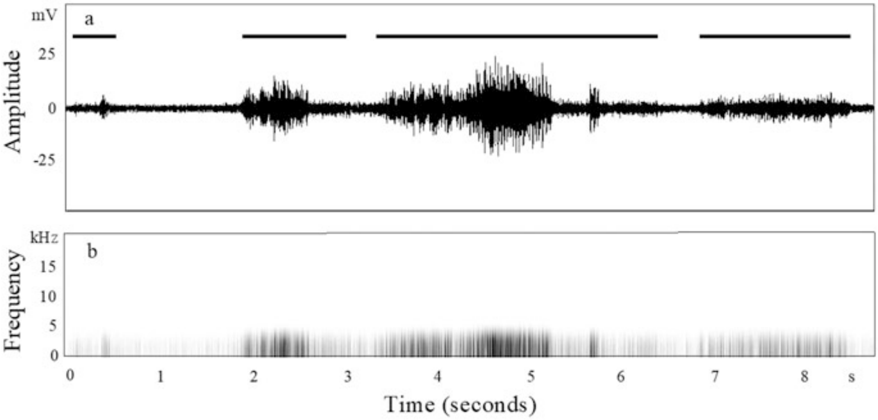

**Fig. 5.12** The vibrational properties of the provisioning call. An oscillogram (**a**) of a segment of a provisioning call is shown. The provisioning call consists of a repetition of clusters of waves with varying range and amplitude. Substantial vibration parts with higher amplitude and other parts with lower amplitude or background noise repeatedly appeared, matching the intermittent sound occurrence (sound bouts: marked with bold horizontal bars) heard by the observer. A spectrogram (**b**) of the same segment of the provisioning call is shown below. Adapted from Nomakuchi et al. (2012)

maintain higher amplitude for 2–130 s, probably indicating audible parts, while the gap parts may represent the less audible segments with lower amplitude. Figure 5.12b shows the spectrogram from the FFT analysis of the same segment, indicating that, consistent with the waveform, the power spectral density was apparently concentrated on a relatively lower level of frequency, varying somewhat in power and frequency.

On the other hand, we compare the power spectra of the same segment of the collected call as above with another segment which was collected when the female was absent from the same nest (as background noise) to identify the actual components of the spectra of the call (Fig. 5.13a, b). The component of power spectrum of the provisioning call can be clearly discriminated from that of the background noise with an occurrence in the range of 0–1 kHz. This result suggests that the provisioning call is basically composed of substrate-borne vibration, although partially including airborne sound, probably as a by-product. This may be supported by the fact that this insect has no auditory senses that can capture airborne sound; it can only receive vibrational senses for substrate-borne vibration (Takanashi et al. 2019).

Observations in the laboratory indicate that the provisioning call apparently comes from females. How do females emit the provisioning call? Calling females were shaking their bodies, maintaining a narrow gap between the dorsal abdomen and wings, suggesting that the females may emit the call from this body vibration. However, it is still unknown how females produce the call. All we know at present, besides the body vibration, is that the body part likely related to production of the call is a complex “membrane” structure on the abdomen. They have an exposed membrane between the thorax and abdomen on the dorsal side under their wings

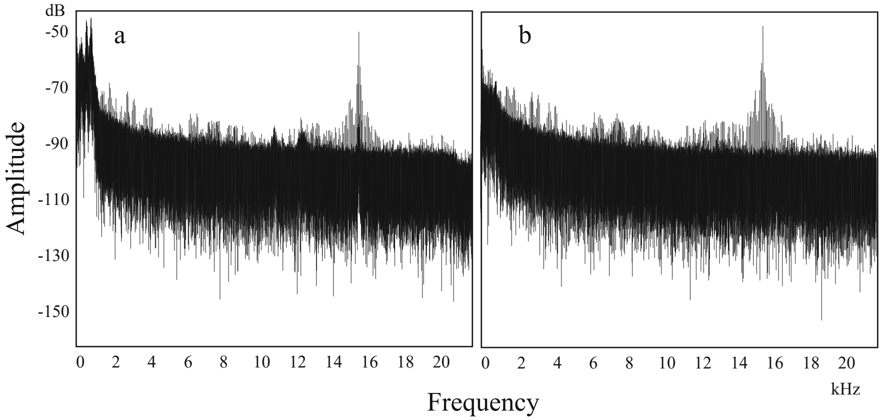

**Fig. 5.13** The power spectra of a segment of the provisioning call when a female was calling in her nest (**a**) and of background noise when the female was absent from the same nest (**b**). The substantial component of the provisioning call that could be clearly discriminated from the background noise is recognized in the lower range of 0–1 kHz. Adapted from Nomakuchi et al. (2012)

(Fig. 5.14). Further, inside their body near the dorsal abdomen, multiple coeloms divided by another internal membrane spread from the small cavity under the exposed membrane between the first and second dorsal abdominal tergite. When we slit the exposed membrane experimentally, the amplitude of the call was

**Fig. 5.14** Dorsal abdomen of female specimen with the four wings removed. Dorsal abdomen has a characteristic membrane between the first and the second tergites. This exposed membrane seems to play a role in amplifying the call emitted by females because the volume of the call was extremely reduced when it was slit or hardened by super glue

extremely reduced, although the call could still be heard. Thus, it seems that the exposed membrane is the organ that functions to amplify the call, not to produce the call, as the call producing "timbal" in some hemipteran insects like cicadas. Although the precise role this membrane structure plays in the provisioning call remains unknown, we expect that it has an important function for the emittance of the call.

It has already been reported that every *P. japonensis* individual produces an "alarm call" when stimulated by touching and blowing on a hibernating group of bugs. The alarm call could be a high pitch (about 10 kHz) stridulatory sound made by scraping the edge of the scutellum and forewing (Filippi-Tsukamoto et al. 1995b). Even if a few individuals of a group are stimulated by attacks of vertebrate predators, their responsive body movements involved with the stridulatory sound gradually expand throughout the group, often leading to large responses by the whole group. As the alarm call eventually emerges simultaneously from every individual in the group, it could become a loud sound, loud enough even for human observers to be able to hear clearly from about 1 m away. By the way, since it is known that *P. japonensis* has no auditory senses for airborne sound (Takanashi et al. 2019), then who hears this alarm call? It could be that the call is meant to startle vertebrate predators, e.g., birds and mammals, instead of alarming conspecific group members. Because *P. japonensis* has triglycerides that are presumed to be unpalatable or poisonous to vertebrate predators (Tojo 2008), this alarm call could be considered to function as a kind of aposematism like the sounds of rattle snakes.

The provisioning call is entirely different from this alarm call. Although the provisioning call was slightly audible to human observers, it may have a functional role mainly as a substrate-borne vibration because most of the sound power was distributed in the lower frequency (less than 1 kHz) range. Further, nymphs might be able to receive a substrate-borne vibration sound more easily than an air-borne sound, because they are usually hiding in the complex inner substrate of the nest, in crevices of debris, fragments of broken and half decayed leaves or tree twigs, in the nest. They may sense substrate-borne vibration better through their legs while standing on a piece of debris in the nest. It is also known that individuals of *P. japonensis* actually have special organs to sense vibration, the chordotonal organ, in their legs instead of senses for recognition of audible sounds (Takanashi et al. 2019). In fact, Gogala et al. (1974), in a leg removal experiment, reported that males in a closely related family, Cydnidae, in which *P. japonensis* was included until Sweet and Schaefer (2002) elevated the genus *Parastrachia* to a new family, Parastrachiidae, need their legs to receive a rival's vibrational call.

It is generally known that individuals in Cydnidae have two mechanisms to produce sound or vibration in communication, a tymbal mechanism and stridulation (Gogala et al. 1974). Tymbal vibration typically has relatively lower frequency signals, which would be effective in communicating through substrate-borne vibration. On the other hand, stridulatory sound has higher frequency signals, which would be effective in communicating through airborne sound (Gogala 1985). We have not yet established which part of the body of female *P. japonensis* is responsible for this vibration production. However, several findings in the present study suggest that the tymbal mechanism could be responsible for the provisioning call for the following reasons. First, the provisioning call basically ranges in the lower region of frequencies that are not usually included in the stridulatory sound in Cydnidae (Čokl et al. 2006). Second, *P. japonensis* has a characteristic membrane structure in the dorsal part of the abdomen, including not only the tergal membrane between the first and second tergum of the abdomen but also an internal membrane structure separating a number of vacant chambers within the abdomen. These membranes could contribute to the vibration production and/or amplification, as Gogala (1985) mentioned about a tergal tymbal in Cydnidae. Third, we also observed that females of *P. japonensis* appeared to vibrate their abdomen while maintaining a small gap between the abdomen and wings, when emitting the provisioning call (unpublished). Therefore, we suspect that the provisioning call could be produced by the membrane structure as the tymbal system.

### *5.3.4 Function of the Provisioning Call*

Why do females emit the provisioning call? From the fact that females begin to call only when they return and enter their nest with a drupe and end the call when they give the drupe to nymphs in the nest, we formulated a hypothesis that the provisioning call functions to call nymphs hiding deep in the crevices in the nest to gather on a drupe. We carried out an experiment using a playback call to test this hypothesis.

As the playback call for the experiment, we employed a vibration sequence (5 min) made by repeatedly combining a specific segment of an actual provisioning call recorded in the Hinokuma field (about 30 s) that contained minimal background noise. We played this constructed playback call to all families in the experiment, assuming that the specificity of the provisioning call for individual families, if present, may be weak because of how remarkably irregular the pattern of actually recorded provisioning calls was even for a given female. To carry out the playback experiment, we used wild families that were collected from the Hinokuma field site and maintained individually in nest cups in incubators as described above. We set the nest cup on the observation table. We placed a drupe at the center of the nest after removing the leaf covering on the nest and connected one end of a steel probe to the drupe and the other end to a contact speaker (Ceramics speaker unit “CEMI,” SANEI HOUSE Co. Ltd., Sagamihara, Kanagawa, Japan) in order to transmit the playback call in the nest through the drupe and any nest debris.

We prepared 29 families with 27.3 ± 6.2 (mean ± SD) individuals of third instars whose mothers were removed from the nests. We exposed each family to two conditions, a drupe with no call (control) and a drupe with the playback call (treatment), sequentially with an interval of 24 h between the two conditions. We changed the order of the conditions to eliminate any order effects: the first 15 families were given the treatment condition first and then the control condition second, and the remaining 14 families were given the control condition first and then the treatment condition second. The response of nymphs to these conditions was

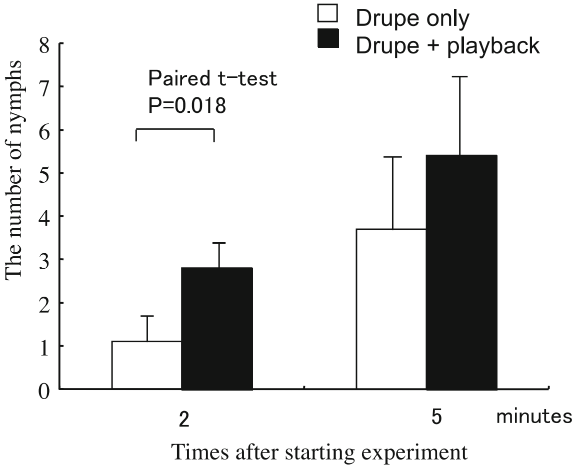

**Fig. 5.15** The effect of the provisioning call to nymphs. The numbers of nymphs that gathered on and clung to a drupe placed in a nest under the conditions with a playback of the provisioning call (shaded columns) and with no call (open columns) at 2 and 5 min after the start of experiment are shown. A significantly greater number of nymphs had gathered on the drupe with the call than that with no call at 2 min after start of the experiment. Error bars represent standard error. Adapted from Nomakuchi et al. (2012)

assessed by counting the number of nymphs that had gathered on the drupe at 2 and 5 min after the start of the trial (setting a drupe and probe in the nest for the control condition and starting the playback call additionally for the treatment condition), respectively.

We obtained relatively clear results from this experiment. Significantly greater numbers of nymphs under the treatment condition (about 10% of total nymphs in the family) in which the nymphs were exposed to the drupe and the playback call at the same time gathered on the drupe, compared with those under the control condition (about 4% of total nymphs in the family) (only a drupe) at 2 min after the start of the trial (Fig. 5.15; paired *t*-test: $t = 2.505$, df = 28, $P = 0.018$). On the other hand, at 5 min after the start of the trial, the difference in the number of nymphs that gathered on the drupe between the treatment and control conditions was not significant, although the average number of nymphs under the treatment condition tended to be greater than that under the control condition (paired *t*-test; $t = 1.106$, df = 28, $P = 0.278$). The statistical significance for the result at 2 min after the start of the trial was consistent even when the Bonferroni method for multiple comparisons was employed. This suggests that at least in the earlier period from the start of the provisioning call, the number of nymphs gathering on a drupe is enhanced by the call.

The hypothesis that the provisioning call functions to call nymphs hiding deep in the nest to gather on a drupe was supported. However, the role of the provisioning call was not definitively established because when the nymphs in the nest were exposed to only the playback call without a drupe, there was a lesser tendency for them to gather on or near the probe (Nomakuchi, unpublished). This means that the call alone does not attract nymphs to a drupe. It seems that nymphs may need the odor of drupes as a cue to recognize the existence of the drupe and/or to locate where it is. What actually is the provisioning call doing to enhance the attractiveness of a drupe to nymphs when it is accompanied by the call in a nest? Our second hypothesis to address this question was that the provisioning call may function to provide nymphs with information about the mother's return to prevent nymphs from dispersing or continuing to hide inappropriately, misidentifying the female as an enemy when she enters the nest with a drupe. In the field, predators such as carabid beetles sometimes intrude in the nest, in which case the nymphs should disperse from their nest or remain hidden inside the crevices of debris (Filippi-Tsukamoto et al. 1995; Nomakuchi et al. 2005). Therefore, it would be adaptive for nymphs to receive a signal that would allow them to recognize when their mother enters the nest, such as the provisioning call, so as to avoid inappropriate dispersal or hiding when they could be feeding.

It is likely that the provisioning call may also have the effect of not only stopping useless evasive behavior of nymphs when the female returns to their nest but also synchronizing feeding on the drupe in the early period. This could lead to several adaptive results, such as enhancing feeding efficiency of nymphs. To understand why, it will be helpful to explain how nymphs actually feed on a drupe. Nymphs feed on the endosperm enclosed by the hard shell in a drupe (Nomakuchi, unpublished). Similar to other heteropterans, *P. japonensis* nymphs insert the proboscis, inject saliva containing digestive enzymes, and suck up the digested liquid endosperm (Shuh and Slater 1995). If the drupe is too hard for a single or a few nymphs to manage, or saliva from a single or a few nymphs is not enough to digest the endosperm, then the feeding efficiency for individuals should increase by group feeding (Kalin and Knerer 1977; Tsubaki and Shiotsu 1982; Lawrence 1990). In fact, the more nymphs that fed on a drupe together, the more liquid was obtained per nymph on average (Nomakuchi, unpublished). Therefore, the effect of the provisioning call may include a factor of enhancing nymphal feeding efficiency by inducing more nymphs to begin feeding on the drupe simultaneously.

The provisioning call may also reduce variance in feeding opportunity and feeding amount among nymphs. Our observations of the nymphal response when given a drupe in the nest without the provisioning call revealed that nymphs gradually gathered to the drupe, resulting in an asynchrony in the timing of nymphal approach to the drupe, probably according to individual differences in boldness of nymphs, their original location in the nest, and their mobility within the nest debris. This may inevitably cause differences among nymphs in the amount of food acquired from a given drupe, likely having a negative impact on female fitness under sibling competition for food (Mock and Parker 1997; Godfray and Parker 1992). Thus, the provisioning call might also serve as a countermeasure by the mother against excessive sibling competition for food among nymphs.

Another fascinating possibility to explore regarding communication between parent and offspring in this system is that of begging by nymphs. When the female enters the nest, nymphs regularly climb on her body, probing it with their proboscis. In response, the mother typically rocks her body from side to side and shakes them off. However, we have also observed on many occasions groups of nymphs gathered and feeding on a female carcass, much as they would feed on a drupe. We assume these are females that had recently died or become too weak to shake the nymphs off. In fact, a preliminary study in which an anesthetized female was presented to a group of nymphs, the nymphs quickly gathered on the female and probed her. After about an hour, the weight of the female had decreased indicating that the nymphs had fed on her. This raises an important question that needs to be explored: is the behavior of nymphs climbing on the female's body, making physical contact with her, and even attempting to probe her with their proboscis, in fact, a form of begging behavior where the nymphs are signaling their hunger to the female? We hope to answer this question in future studies.

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**Hiromi Mukai** another student in Dr. Nomakuchi's laboratory and a clever and enthusiastic researcher with fine observational skills also completed a doctoral degree under Dr. Nomakuchi at the United Graduate School of Agriculture, Kagoshima University, with her excellent work that clarified the process by which egg-guarding females synchronize the timing of egg hatching. She is currently a researcher at the Department of Forest Entomology, Forestry and Forest Products Research Institute.

**Shintaro Nomakuchi** an ecologist focusing on insect behavior, came to Saga University in 1993 as an Associate Professor, and was keen to share his very valuable expertise and join the *P. japonensis* research team, which he eventually headed. The work on clarifying the quality of the habitat, the techniques for monitoring the subpopulations and for carrying out a variety of ecological and behavioral studies, as well as the methods for performing robust data analyses, all got a hefty boost, and we were off and running. He is a Professor Emeritus of the Faculty of Agriculture at Saga University.