Chapter 6
Foraging Strategies

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Abstract *Parastrachia japonensis* Scott (Heteroptera: Cydnidae) females progressively provision nests with drupes of the host tree, *Schoepfia jasminodora*, a scarce, ephemeral, and unpredictable resource. To optimize use of the resource, they have evolved several extraordinary behaviors to increase the success of the only egg mass the female will produce in its lifetime. These behaviors include guarding of eggs and nymphs, trophic egg production, and progressive provisioning. To accomplish provisioning, they have evolved a complex navigation system that allows them to forage repeatedly over great distances and time and successfully return to the nest during both day and night. During inspection of the fickle drupes, females employ a sequence of behaviors that ensure they transport only the best ones to their nest. Females steal from each other while foraging and even raid conspecific nests. In response, defensive behaviors against thievery have evolved. This chapter explores the mechanisms and evolutionary implications of these foraging behaviors that provisioning females use to enhance their fitness.

Keywords Alternative tactic · Chemical cue · Foraging · Kleptoparasitism · Navigation · Orientation · Resource competition · Resource quality · Selective foraging · Visual compass

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6.1 Introduction

Foraging to feed oneself requires the ability to locate and recognize an appropriate food resource, the ability to defend it from conspecific and interspecific competitors, and the ability to process it. Progressive provisioning is a particular type of foraging behavior that requires the provisioning parent to not only be successful in those endeavors but also be able to make repeated trips between the nest and the food source. It occurs commonly in birds and mammals, but, outside the Social Hymenoptera, is rare among insects. In addition to the cluster of cydnids alluded to in Chap. 4, a handful of solitary wasps in disparate genera progressively provision paralyzed insects to the nest to feed larvae (Field 2005), and burying beetles progressively provision larvae (Eggert and Sakaluk 1995; Trumbo 1996, 2012). Earwig females also progressively provision young (Kölliker 2007), as do male assassin bugs (Reduviidae) (Ralston 1977; Machado and Trumbo 2018). As discussed in previous chapters, appropriate food, that is, drupes that are of high enough quality to be worthy of transportation to the nest, are, in most years, very few and far between. The search for an acceptable drupe can take hours and requires traversing a tortuous path over rough terrain and, often in miserable, rainy weather (Filippi-Tsukamoto et al. 1995; Filippi et al. 2002). In this chapter, we first describe the fascinating behaviors that make it possible for *Parastrachia japonensis* Scott (Heteroptera: Parastrachiidae) females to navigate the complex provisioning trip. We then explain the exhaustive process that provisioning females use to determine the acceptability of a drupe.

There are trade-offs and risk-sensitive decisions to be made while foraging (Davies et al. 2012). Provisioning females must compete with the many other provisioning females they encounter in the foraging area, each female with the single goal of securing as many of the precious drupes for its young as it can. We describe the trade-offs involved in nest site preference in terms of provisioning efficiency and the risk of losing drupes to females who employ an alternative tactic of stealing (kleptoparasitism) over self-foraging, as well as how females defend themselves against theft of drupes from the nest. Finally, we explore whether kleptoparasitism arises as a purely opportunistic behavior or whether it has evolved as an alternative tactic in the larger provisioning strategy.

6.2 Visual and Chemical Orientation in the Provisioning Excursion

6.2.1 *Navigating the Provisioning Trip*

As described in previous chapters, during the provisioning season in June, females of the shield bug, *P. japonensis*, nest under fallen leaves and excavate a small hole as a nest under the leaf litter where they lay their eggs, and then guard the egg mass.

Unless there is an accident, the bugs do not leave the nest during the 2 weeks of egg protection (Filippi-Tsukamoto et al. 1995). Nests are built at a depth of at least 5 cm below the ground surface, and some nests are built under a single fallen leaf. Perhaps because of this, the nests do not have a clear tunnel structure, and the entrances to the nests that they enter and exit are not made of compacted soil, but rather look like gaps in fallen leaves (Fig. 6.1).

The nests are usually built a few meters, or in some cases more than 20 meters, away from the host tree, *Schoepfia jasminodora* (Santalales: Schoepfiaceae) (Filippi-Tsukamoto et al. 1995). Because of the spatial distribution of the nests and host trees, females must first move several meters or more to reach a host tree under which the drupes for the nymphs to feed on have fallen. How do they find this foraging area and the drupe? Next, after finding the drupes of the host tree, the females must return without error to their own nest. In the forest, it is almost impossible for us to find the nest entrance of *P. japonensis* which has no identifiable cues. The nest entrance is a small opening with a diameter of about 1 cm between overlapping fallen leaves on the ground surface and appears to have no identifiable visual characteristics. How do the females reach their nest after searching for food? The navigation task of finding a goal such as a nest or a drupe on such a two-dimensional surface is called x, y-orientation (Dyer 1998). In this section, we present what is known about the mysteries of the navigational task during provisioning excursions in *P. japonensis*.

In late June, when the nymphs hatch, the female walks out of the nest, finds the drupes under the host tree, and brings them back to the nest at our field site, Mt. Hinokuma Park (Tsukamoto and Tojo 1992). For example, during the provisioning season of 2000, provisioning behavior was observed at a 15 × 15 m study site at noon; females searching for drupes were first observed on June 19 and peaked on June 26, and the last provisioning female was observed on July 9 (Hironaka et al. 2003b). During this observation period, 10 days were sunny, 8 days were cloudy, and 3 days were rainy, but provisioning behavior was observed regardless of the weather conditions. We also counted females searching for or transporting drupes at the study site for 24 h at 2-h intervals during the peak of the provisioning season.

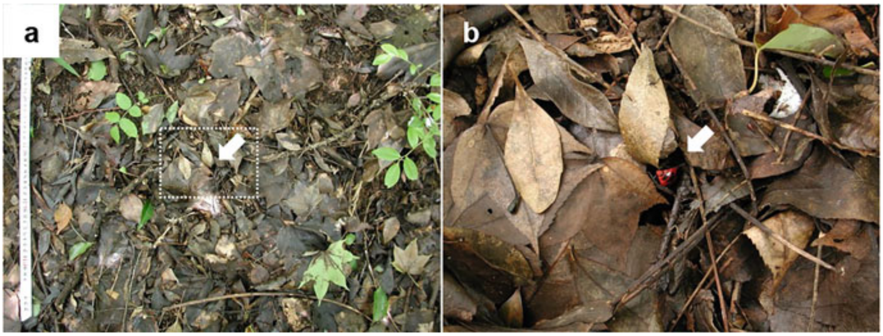


Fig. 6.1 A typical nest entrance (**a**) and the female peeking out of it (**b**). The area of the dotted line is enlarged and shown as (**b**). The nest entrance is typically about 1 cm in diameter, which allows the female to pass through. Arrows indicate an entrance on the ground

Many females were observed regardless of the time of day, indicating that they were provisioning not only during the day but also at night.

Field observations of the paths of the provisioning excursion of females who had experienced drupe transporting many times revealed that they achieved a very interesting path from leaving the nest to returning to the nest (Hironaka et al. 2007a, c). After leaving the nest entrance, the female first started walking toward the direction of the host tree. It appeared that all females had a predetermined direction for foraging when they left the nest. However, their walking paths were quite tortuous. If no drupes were found where they were headed, they walked in a complex path over a large area. When the female finally found a drupe with sufficient endosperm to merit being transported to the nest (Nomakuchi et al. 1998; also see next Sect. 6.3), it always oriented toward its own nest in a straight line close to the shortest path (Fig. 6.2; Hironaka et al. 2007a). When the female reached the vicinity of its own nest, it started to search around the nest entrance. We call the stage from the departure from the nest to the discovery of a drupe the foraging phase and the stage from the start of drupe transport to returning to the nest the homing phase.

Apparent differences between the orientation behavior of the foraging and homing phases were observed. In the foraging phase, the bug left for the previously foraged point, frequently changing direction. Sometimes it stopped walking and raised and waved its antennae. On the other hand, in the homing phase, the drupe-

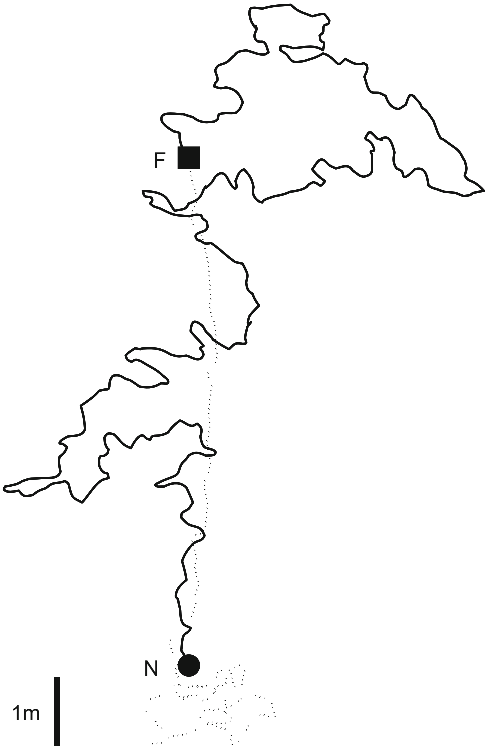


Fig. 6.2 A typical example of a diurnal provisioning excursion of *P. japonensis*. The continuous and dotted lines indicate the foraging and homing paths, respectively. The bug searched arduously until it encountered a drupe. After accepting a provided drupe, it took a direct path back to the nest over coarse terrain (dotted line). N (black circle): nest; F (black square): location where the bug discovered the drupe. Adapted from Hironaka et al. (2007a)

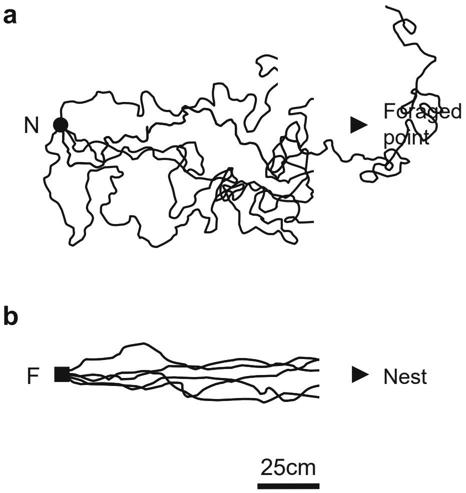


Fig. 6.3 The walking paths in the foraging and homing phases. We plotted the foraging (**a**) and homing (**b**) paths of five individuals to a distance of 1 m. N (black circle): nest; F (black square): location where the bug discovered the drupe. Arrows indicate the direction of the goals of each phase

laden bug walked rapidly, straight to its nest. Thus, the walking paths in the foraging phase clearly differed from those in the homing phase. The foraging bug showed a winding path, and, as a result, its path covered a wider area compared with that of the homing bug (Fig. 6.3; Hironaka, unpublished data). We measured the walking speed and the degree of curvature of the paths of 23 individuals who were repeatedly provisioning in the field (Hironaka, unpublished data). The walking speeds in the foraging and homing phases were 71.7 ± 19.8 (mean ± SD) cm/min and 86.4 ± 23.6 cm/min, respectively. The foraging speed was significantly slower than the homing speed (Wilcoxon signed-rank test: $P = 0.0007$). The sinuosity indexes of the paths taken in the foraging and homing trips were 1.6 ± 0.3 (mean ± SD) and 1.1 ± 0.1, respectively. The sinuosity of the foraging trip was significantly higher than that of the homing trip (Wilcoxon signed-rank test: $P < 0.0001$).

6.2.2 *Outbound Trip*

As described in Chap. 3, female *P. japonensis* develop their ovaries by feeding on the endosperm of drupes on host trees for 1 week to 10 days. When the ovaries are fully developed, the gravid female descends from the tree and searches for a nesting site while walking away from the host tree. However, exactly how this behavior of departing from the tree is carried out has not been sufficiently observed. The female roams through the fallen leaves to find a suitable place to build a nest with a thick layer of leaf litter; it burrows into the leaf litter to create a small chamber in which it can barely change its posture and lays a single round egg mass. The eggs hatch approximately 2 weeks later. The female usually leaves the nest within 48 h after hatching to perform the first provisioning behavior.

In order to find drupes to feed its nymphs, the bug must orient itself and reach an area under the host tree that serves as the foraging area of provisioning female *P. japonensis*. During the provisioning period of 2003, many host drupes were scattered over the ground, and 13 nests were discovered in the study site (Fig. 6.4; Hironaka, unpublished data). The total number of drupes around the four host trees was 307. Of these 307 drupes, 116 (37.8%) had an endosperm that was at least 50% developed and were considered to be good drupes. Some drupes fell from the tree and rolled out of the crown area (the area of ground directly under the crowns of the four host trees). The drupes were distributed over the uneven ground in a pattern of loose patches (foraging area), and no notable differences in the distribution of good and bad drupes were observed. Nests were observed along the periphery of the foraging area. In 2006, we observed the drupes and nests and recognized the same tendencies regarding the distribution and quality of drupes.

If a female memorizes some kind of positional relationship between the host tree and its own nest when it searches for a nesting site, it will be able to orient toward the direction of the relevant foraging area without losing its way after leaving the nest, even on its first provisioning bout. However, based on several observations of first-time provisioning behavior, we expect that the female will not remember the direction and distance of the host tree on which it was feeding 2 weeks ago. The first time a female left the nest, it went out in a random direction relative to the

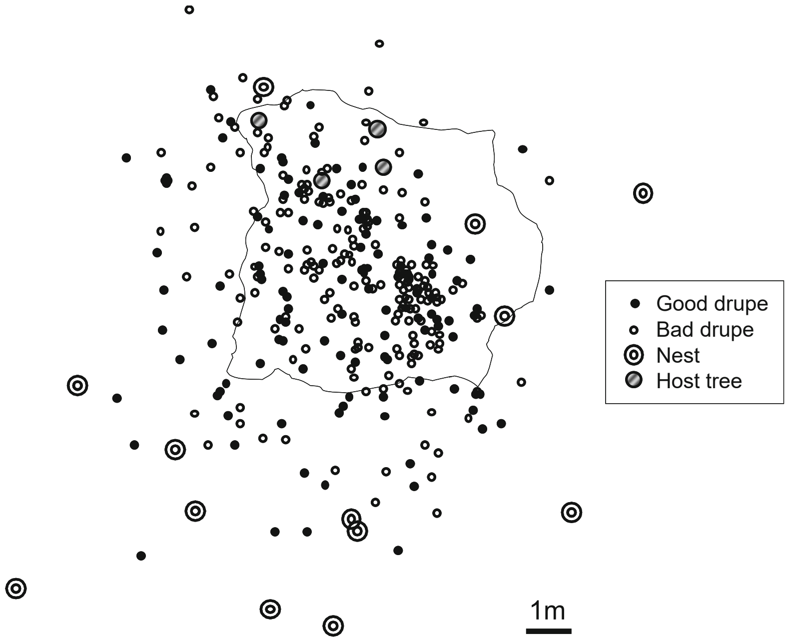


Fig. 6.4 A map of the fallen drupes and nests around the host tree at the busiest provisioning period in 2003. The solid line outlines the area of ground directly under the overlapping crowns of the host trees

direction of the nearest host tree (Hironaka et al. 2007c). As a result, the female repeatedly searched around the nest and returned to it empty-handed without ever reaching the foraging area. We expected that the female would gradually expand its search direction and range and eventually reach the foraging area. Once a female arrives at the foraging area under the host tree and discovers a drupe, it is able to orient toward the direction of the host tree during the next foraging phase (Hironaka et al. 2007c). However, we were able to set a “foraging area” in the absence of the host tree and train the female, whose entire nest, along with the female, we had transported to the constructed foraging site. This led us to believe that bugs do not aim in the direction of the host tree. Therefore, we conducted an experiment to distinguish whether the bug was heading toward the host tree or returning to the place where it had found the previous drupe before (Hironaka, unpublished data). To clarify which of the two directions a bug orients toward, we experimentally established the condition whereby the direction to the host tree does not correspond with the direction to the previously foraged point (Fig. 6.5a). We chose several nests and laid twine between each nest and the nearest host tree. The direction to be foraged (foraged direction) was determined as an angle of 45° counterclockwise to the twine of the nearest host tree, and we laid the twine on that path. Under natural conditions, we looked for a bug which had successfully conveyed a drupe and chose only those females that found the drupe within an angle of 40°, centering on the host tree direction. Next, we tracked the second foraging trip of the selected females and

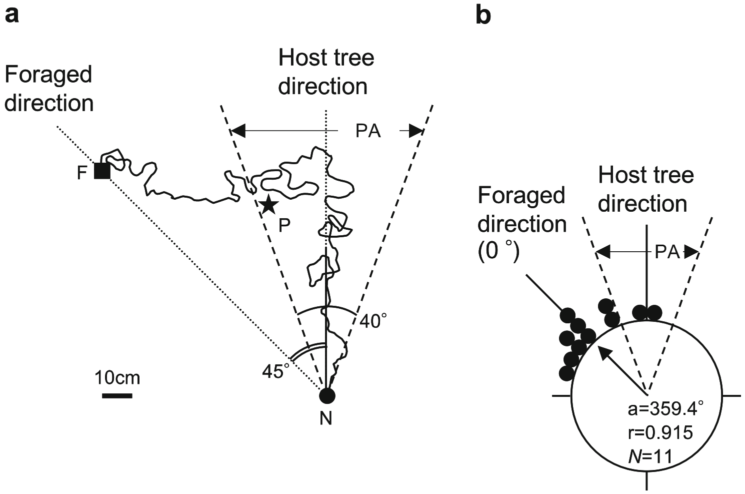


Fig. 6.5 A schematic drawing of the experiment (**a**) and the distribution of foraged directions (**b**). The locations of the nest and of the drupe found in the first run are denoted by N (black circle) and P (black star), respectively. On the first trip, the bug discovered a drupe in the area within an angle of 40° centering on the host tree direction, as shown by PA. The solid line shows an example of an actual foraging path, and F (black square) shows the location foraged on the second foraging trip. Solid circles in b indicate orientation angle for each bug. The arrow indicates mean vector. *a* mean angle of orientation; *r* length of the mean resultant vector; *N* number of animals tested

waited until each bug crossed the twine representing the previously foraged direction. When the foraging female crossed the twine, we gave it a drupe, and it started to home to the nest. Using this experimental procedure, the angular differences between the foraged points of the first and second trips were never less than 25°. When the female started the third foraging trip, the direction of departure from the nest at a distance of 0.5 m was measured. A bug that found a drupe at a location in the direction of the host tree on the first foraging trip homed along the line between the host tree and its nest. On the second trip, the bug roughly oriented toward the previously foraged point (P in Fig. 6.5a). A typical example of a foraging path taken on the second foraging trip is shown by the solid line in Fig. 6.5a. We waited until the bug crossed the line of the determined previously foraged direction and gave it a ripe drupe (F in Fig. 6.5a). Figure 6.5b shows the orientational direction individual females took on the third trip (filled circles). The figure reveals significant clustering in the previously foraged direction (V test: $P < 0.0001$). This result shows that *P. japonensis* females did not leave for the host tree, but that they, instead, oriented toward the direction where they had obtained a drupe on the most recent foraging trip.

In the final stage of the foraging phase, females use the odor of the ripe pulp as a cue to find good drupes, as shown by Y-tube experiments (Nomakuchi et al. 1998). This will be explained in detail in the next Sect. 6.3. Drupes filled with endosperm release volatile chemicals such as ethyl acetate, acetic acid, and ethanol when the pulp ripens (Hironaka, unpublished data). It is inferred that the female eventually reaches the host drupe after being attracted by these chemicals.

6.2.3 Inbound Trip

Upon reaching the drupe, the females assess it for tens to hundreds of seconds (Nomakuchi et al. 1998). When a female determines that the drupe is good enough and should be provisioned, it immediately begins to return to its nest. At this time, the bug looked around once at the location where the drupe was found and then walked out with its longitudinal body axis set roughly in the direction of the nest. The female did not lose sight of the nest's direction and returned to it along a straight path, even though she walked over and around various obstacles on the ground surface along the way. As a rule, once females reached the periphery of their nests, they made a sharp turn and then switched to a searching behavior in which they frequently changed direction (Fig. 6.6; Hironaka et al. 2003a, c). In other words, the homing behavior of *P. japonensis* consists of two phases: a "straight run phase" to reach the periphery of the nest and a "wandering phase" to search for the nest in the immediate vicinity of the entrance.

We measured whether homing behavior changed between provisioning periods in the field (Hironaka et al. 2003a). Two parameters that indicate the accuracy of orientation, "homing direction" and "starting position of wandering behavior," were examined in early females within a few days of the start of provisioning and in later females 10 days after the start. The homing direction was defined as the

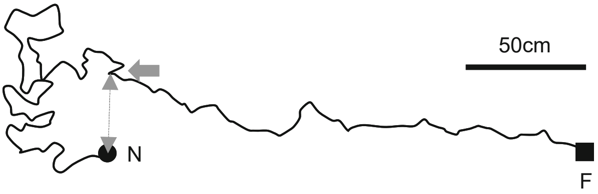


Fig. 6.6 A typical homing path of *P. japonensis*. N (black circle): nest; F (black square): location where the bug discovered the drupe. After direct homing for ca. 2 m, the bug usually performs a sharp turn (see arrow) and switches its behavior to search. Dotted line indicates the length between the 'wandering point' and its nest entrance. Adapted from Hironaka et al. (2003a)

direction of the body axis of the females 1 min after they began walking. The starting position of the wandering behavior was defined as the straight distance from the nest entrance to the wandering point (Fig. 6.6). At the same time, we measured the "wandering time," which is the time from the start of the searching behavior to the final arrival at the nest entrance. The results showed that there were no differences in the homing direction (*V* test: earlier homing, $P < 0.0001$; later homing, $P < 0.0001$) and the starting position of wandering behavior (Mann-Whitney *U* test: $P = 0.209$) between earlier and later homing and that both females that carried a drupe for the first time and females that carried them repeatedly returned along a straight path toward their own nest (Fig. 6.7a–c). On the other hand, a significant difference was

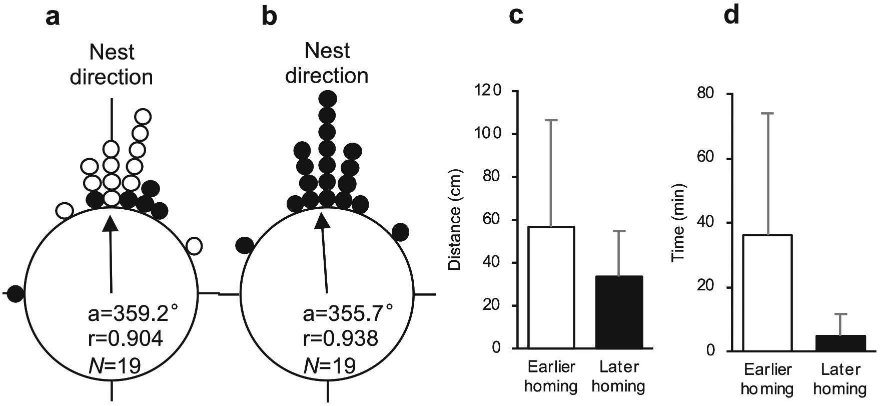


Fig. 6.7 Behavioral elements during the homing phase in the earlier and later provisioning periods. Circular graphs showing the distribution of "homing direction" of earlier (**a**) and later (**b**) homing bugs. Small circles around the circular graph indicate the 'homing direction' of individual bugs. White circle in the earlier homing graph (**a**) shows the homing direction of initial homing bug. Arrows indicate the mean resultant vectors (*a* mean direction of the resultant vectors, *r* the radius of the circle corresponds to vector length = 1, and *N*; sample size). The distances between the "wandering point" and the bug's nest (**c**) and the "wandering time" (**d**) were also measured. Mean values with SD (vertical bars) are represented in the histogram. Adapted from Hironaka et al. (2003a)

observed in the wandering time to finally arrive at the nest entrance (Fig. 6.7d). The wandering time for the nest was dramatically reduced from an average of 36.1 min in the earlier homing to 4.7 min in the later homing (Mann-Whitney *U* test: $P < 0.0001$).

6.2.4 Chemical Cue Used in Nest Searching

What cues do *P. japonensis* use to finally reach their own nest during the wandering phase? We conducted a field experiment to determine whether odor is an important cue in the final stage of the inbound trip as it is in the outbound trip. In the wandering phase, we blocked the compound eyes and/or antennae of homing females with paint and released them near the nests to determine whether they could enter their own nests (Hironaka et al. 2007a). Females whose eyes were covered with silver paste found the nest entrance and entered through it. On the other hand, the females whose antennae were covered with watercolor paint did not notice the nest entrance even when they passed close by it. The nest contains the odor of the nymphs, the provisioned drupes, and the female's own odor. We conducted an experiment to determine which odor was used as a cue for the female to return to its own nest (Hironaka et al. 2007a). We placed a gravid female in an individual lidded, clear plastic cup filled with substrate (leaf litter), where it deposited an egg mass and cared for its nymphs upon hatch (Fig. 6.8). After the start of provisioning behavior, we created four other artificial cups by placing nymphs and substrate in the new cups while the female was out of the nest. The four new nests consisted of the female's own nymphs and own substrate, nymphs of another female and the original female's substrate, the female's own nymphs and alien substrate, and alien nymphs and alien substrate. When these were presented to the female in the wandering phase, it returned not only to the nest of its own nymphs and substrate but also to the nest of its own substrate, although the nymphs had been replaced by those of other individuals. This strongly suggests that the substrate that comprises the nest and its surroundings contains cues used by the female to orient toward its own nest.

So, what kind of substrate cues are there? We suspected that the nest substrate might have some kind of odor emitted from the female itself. When rearing *P. japonensis* in artificial nests using Kimwipes® as a substrate, the white Kimwipes® turn into a brownish color and have a distinctive sweet smell that becomes stronger as the days pass. When we attached a centrifuge tube to the anus of the female, we found that it excreted yellowish-brown excrement at intervals of several days during the egg protection and provisioning periods (Fig. 6.9). We hypothesize that this excrement serves as an individual identification pheromone to distinguish its own nest from other nests. This hypothesis that the female gradually marks the nest with her own excrement nicely explains the shorter wandering time in the later stages of the provisioning period. These facts indicate that chemical cues derived from the nest substrate play an important role at least in

Fig. 6.8 A photograph of the artificial nest used in the experiment. Red granular objects are second instar nymphs aggregating on a black ripe drupe. Each egg-guarding female was reared in a clear plastic cup lined with substrate. The cup was covered with a perforated plastic lid to prevent escape. After eggs hatched, we continued to rear them together with their mother and ripe drupes, until the experiment

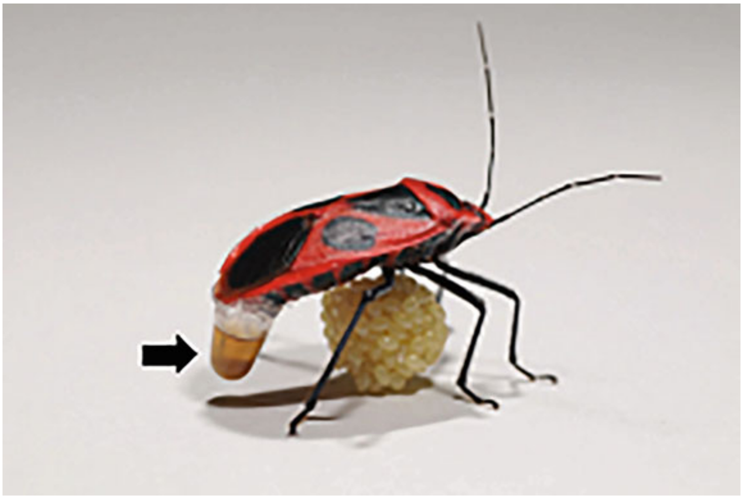


Fig. 6.9 An egg-guarding female with excreta being collected. A centrifuge tube was glued over the anus and left there until the end of provisioning behavior. The arrows indicate the excrement accumulated in the container

the final stage of homing. Can the use of chemical cues also explain the homing behavior of the straight run phase of the inbound trip?

6.2.5 Path Integration System

R. Wehner, one of the leading authorities on insect orientation and navigation, suggested that insects performing provisioning navigation use three different navigation systems to return to their starting point, the nest (Wehner and Wehner 1990). One is a path following system, such as a pheromone trail, which follows the outbound path directly, another is a path integration system, which accumulates the direction and distance of its own movement from the starting point, and the third is a map-based system, which stores surrounding landmarks and determines the starting point based on the memories of the landmarks. The easiest way to find out which system a given navigator uses is to conduct a displacement experiment. We artificially displaced a female before homing to another location and observed the path of its subsequent return (Hironaka et al. 2007a, c). We gently picked up a female that was searching for drupes, artificially displaced it to another location, and immediately gave it a drupe. It then initiated homing behavior. If the displaced bug loses its homing direction and wanders around, a path following system might be used. If the bug directly orients to the position where the nest should be, we can say that it is a path integration system. Or, if the bug can precisely relocate to the nest, it is likely to be using a map-based system. What kind of homing path did the displaced bug follow? After being displaced to a location on the opposite side of its nest, the bug did not head for the true nest, but headed directly in the direction of the fictive nest, that is, where the nest should have been if it had been displaced along with the female. When the bug had walked almost the same distance as that between the capture location and its true nest, it made a sharp turn and showed typical wandering behavior (Fig. 6.10; Hironaka et al. 2007c). Day and night, the bugs could not recognize any change in the position of the nest when they were artificially displaced to any location and oriented precisely toward the location where the nest had been before the displacement. The results of this experiment indicate that *P. japonensis* females depend on a path integration system in which the direction and distance of outbound movement are constantly monitored, and the vector accumulated from the outbound path is reversed at the time of homing to form the home vector, in the straight run phase (Hironaka et al. 2007a, c). To the best of our knowledge, this is the first report in the heteropterans of a navigational strategy using path integration system.

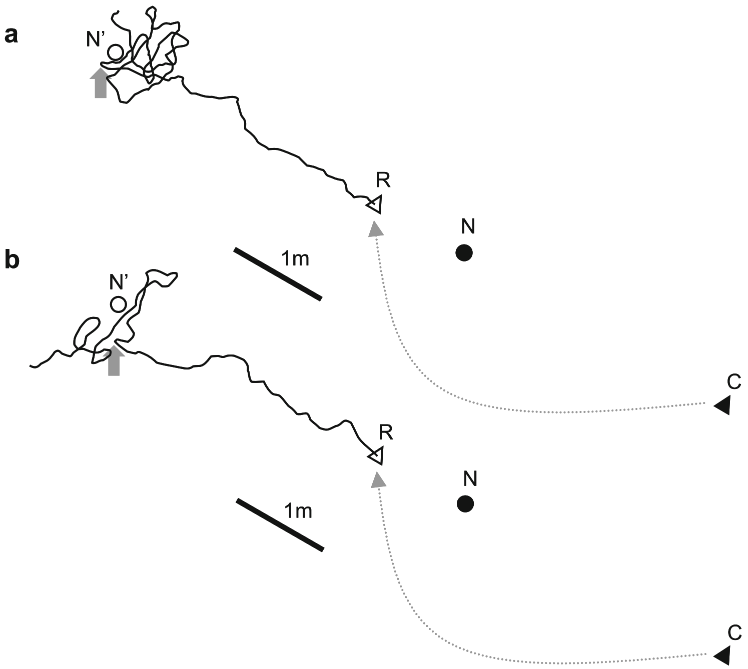


Fig. 6.10 Homing paths in a diurnal (**a**) and nocturnal (**b**) displacement test. An example of the homing path for 10 min. N (black circle): nest; C (black square): point of capture; R (white up-pointing triangle): point of release; N′ (white circle): location of fictive nest (approx. 180° from true nest site). The bug was displaced from C to R (curved arrow). The gray arrow indicates the point where the bug initiated wandering behavior. Adapted from Hironaka et al. (2007c)

6.2.6 Visual Compass Mechanism

Animals that navigate using a path integration system measure the route of their outbound trip from the starting point, such as a nest to the current location using some kind of compass and distance meter, and accumulate direction and distance information (Collett and Collett 2000). In addition, when they return to the starting point according to the homing vector obtained by path integration, navigators check whether the orientation direction has deviated from the homing vector and how much of the distance in the homing vector it has consumed. In other words, navigators always need directional and distance information in the outbound and inbound trip. Here is what we know from field and laboratory experiments about the cues from which *P. japonensis* obtain directional information.

It is known that insects obtain directional information from various environmental cues such as the sun, polarized light in the sky, geomagnetism, wind, and idiothetic cues (Wolf 2011). Which of these mechanisms does *P. japonensis* use? We first conducted a field experiment to determine whether vision of *P. japonensis* plays an important role in the reception of direction or distance information. We applied a light-blocking silver paste to the compound eyes of a female just before it started its homing trip and examined whether it was able to orient toward its nest. We drew a circle with a radius of 50 cm centered on the foraged point, the starting point for returning to the nest (homing), and investigated which point on this circumference the bug would reach (Fig. 6.11a; Hironaka et al. 2003b). The orientation angle of the bugs whose eyes were coated with transparent enamel was distributed around the direction of the nest, indicating that all the bugs headed for the nest accurately (Fig. 6.11b; Hironaka et al. 2003b). On the other hand, bugs with their eyes blocked with silver paste oriented toward various directions, and some of them headed for the completely opposite direction to the nest (Fig. 6.11c; Hironaka et al. 2003b). *P. japonensis* identifies the homing direction by looking at something on the forest floor during the daytime.

In an additional field experiment in which the dorsal or ventral half of the compound eyes of homing bugs was blocked, we found that the directional cues were perceived by the dorsal side (Hironaka, unpublished data). To investigate the possibility that *P. japonensis* females use the sun compass, which is used by many insects (Wehner 1984), we had bugs perform provisioning behavior in a laboratory arena with a single bulb-shaped fluorescent lamp. In the arena, the bug repeated its characteristic foraging and homing behavior, which was the same as in the field. When the position of the light source was shifted by 180° horizontally during the

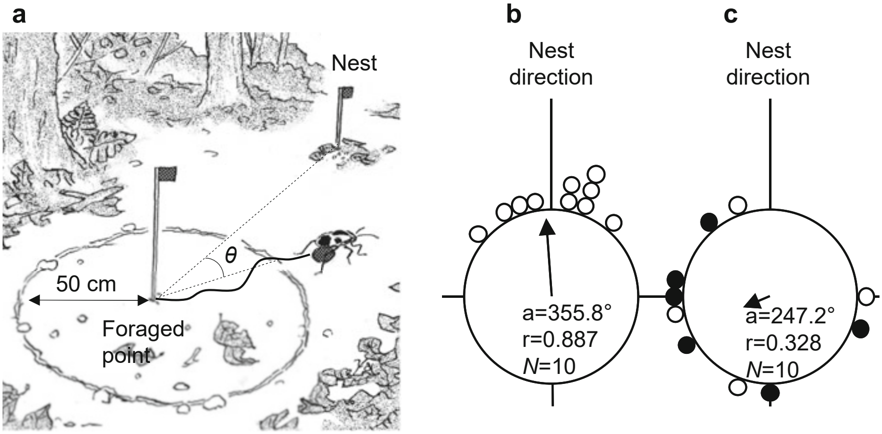


Fig. 6.11 Schematic representation of direction measurement and homing direction during the day. We marked the point arrived at by the homing female along the circumference of a circle with a radius of 50 cm drawn with the foraged point at its center and calculated the orientation angle (**a**). The orientation angle is the angle (*θ*) between the direction of the arrival point and the direction of the nest seen from the foraged point. The distribution of homing directions of females with their compound eyes and ocelli painted with clear enamel (**b**) or silver paste (**c**) are shown on sunny (white circles) and rainy (black circles) days. Arrows indicate mean vector. *a* mean angle of orientation; *r* length of the mean resultant vector; *N* number of animals tested. Adapted from Hironaka et al. (2003b) and Hironaka (2014)

homing phase, the bugs suddenly changed their orientation direction and walked toward the starting point of the homing phase as if they were returning to the path they had walked. From a series of behavioral experiments, it became clear that *P. japonensis* females can use light sources as compass markers in the daytime (Hironaka et al. 2007b).

However, as mentioned earlier, *P. japonensis* can return to its nest with a straight path even at night, when the sun compass is not available, using a path integration system (Hironaka et al. 2007c). Therefore, we conducted a similar eye-blocking experiment to determine whether the visual compass was also used at night. Females that had their eyes blocked with silver paste lost the homing direction regardless of the nighttime weather (Hironaka et al. 2003b).

6.2.7 Canopy Cue in Nocturnal Homing

What do provisioning *P. japonensis* females look at in the forest at night to obtain directional information? The first possibility to consider is celestial cues, such as the moon and stars (Wehner 1984), and the pattern of linear polarization in the night sky due to moonlight (Dacke et al. 2003). These celestial cues are often used to navigate by flying insects and insects that live in open environments such as desert and sandy beaches. However, in the forests where *P. japonensis* lives, the celestial cues do not provide a stable compass reference because they are surrounded by dense woody vegetation. In fact, bugs accomplish accurate orientations in the foraging and homing phases even on rainy nights when these celestial cues are not available (Hironaka et al. 2003b).

Another overhead visual cue available in the forest is the canopy, the layer of upper branches and leaves of the trees that covers the navigator. In 1980, B. Hölldobler showed experimentally that forest-dwelling ants determine their orientation from images of the surrounding canopy when returning to the nest. He named this behavioral ability canopy orientation as a novel system of animal navigation and reported it in *Science* (Hölldobler 1980). However, to date, little is known about how animals use canopy images, such as whether they look at the entire canopy or just part of it. Furthermore, whether some animals use the canopy as an orientation cue at night has not yet been revealed.

To gain some understanding about this, we went into the forest at night and turned off the outdoor headlights. In the darkness of the forest, we couldn’t see anything for a while, but as our eyes gradually became adapted to it, images of the canopy that surrounded us appeared. Through gaps in the canopy, we could see the night sky, which was only slightly brighter than the canopy. The contrast between the night sky and the canopy created a complex canopy image (Fig. 6.12; Hironaka 2014). Do *P. japonensis* females look at the canopy in the forest at night, and if so, how do they get directional information from the canopy?

If the bug uses the canopy image as an orientation cue, this means that it will be using some part of the canopy as a compass reference. Therefore, we hypothesized

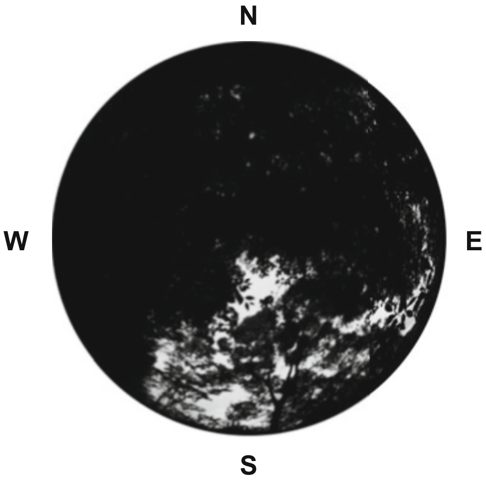


Fig. 6.12 A hemispherical photograph taken above a nest of *P. japonensis*. Canopy gaps of various sizes are scattered over bugs. At this location, relatively large gaps (white areas) were observed from the zenith to the south. Adapted from Hironaka (2014)

that it uses a canopy gap as a compass reference to determine the direction and tested this hypothesis in a field experiment. A box-shaped experimental arena was set up outdoors in a location with little artificial light, and a female was allowed to nest and provision inside the arena (Fig. 6.13a). The sides and ceiling of the arena were covered with dark blue plastic boards, and one circular hole was placed on the south side of the ceiling. The hole and dark blue plastic board simulated the situation where there is one gap opening in the canopy cover. In this arena, we confirmed that a *P. japonensis* female was able to reach the "foraging area" in the center of the arena, assess a good drupe, and then carry it back to the nest. After observing this, the next time the female reached the "foraging area," we rotated the ceiling board by 180° such that the position of the artificial gap was changed from south to north. The female then started to walk in the complete opposite direction to its nest (Fig. 6.13b). In other words, *P. japonensis* used the position of the canopy gap as a compass reference for path integration in the nocturnal homing (Hironaka et al. 2008a, b).

6.2.8 Conclusion: Navigation Ability in Subsocial Bugs

What kind of cues and behavioral mechanisms do insect navigators use to accomplish their navigation? This question has been studied intensively in the hymenopterans, which include bees and ants. Hymenopteran insects build complex nests in which they congregate and live highly social lives. As a result, they exhibit a behavior called central place foraging, in which they go from a central point, such as a nest, to feeding sites, obtain food, and then return to the central point again. To accomplish this provisioning navigation, it is thought that the hymenopterans have acquired precise orientation ability and various navigation systems. However, provisioning navigation is not the exclusive property of bees and ants. Provisioning

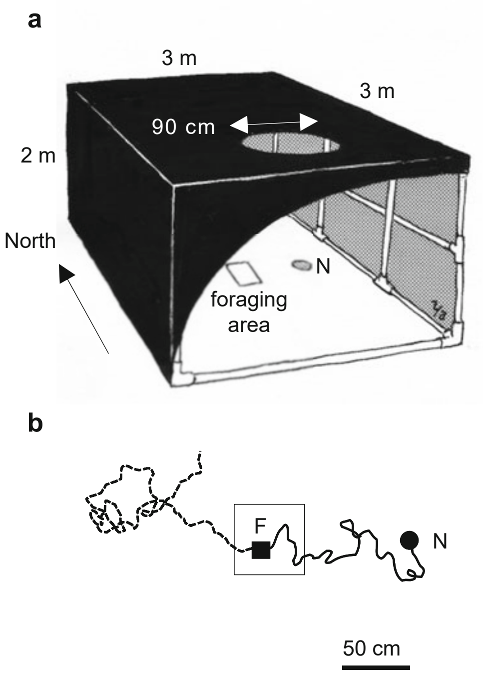


Fig. 6.13 Schematic representation of the experimental arena (**a**) and a typical provisioning path of a bug (**b**). The walls and ceiling were made of dark blue plastic board. A round hole simulating a canopy gap was opened in the ceiling; initially it was positioned south from the center of the arena. A square 'foraging area' containing several drupes was located in the center of the arena. The experimental nests were set on the ground 1 m from the center of the 'foraging area'. The solid and dashed lines indicate the foraging and the homing paths, respectively. N (black circle): nest; F (black square): location where the bug discovered the drupe. Adapted from Hironaka et al. (2008a, b)

navigation has been observed in several species of subsocial bugs, including *P. japonensis*. In addition, several other taxa of subsocial insects, such as burrow-building crickets (Beugnon and Campan 1989) and earwigs (Radl and Linsenmair 1991), also perform provisioning navigation. Among subsocial bugs belonging to Cydnidae and Parastrachiidae (or subfamilies Parastrachiinae), provisioning behavior has been observed in six species: *Sehirus cinctus*, *Adomerus triguttulus*, *A. variegatus*, *A. rotundus*, *Canthophorus niveimarginatus*, and *P. japonensis* (Mukai et al. 2010; Inadomi et al. 2014). In all of these species, the provisioning path from departure to return has been observed. Of these, five species, *A. triguttulus* *A. variegatus*, *A. rotundus*, *C. niveimarginatus*, and *P. japonensis*, have been observed to return to the nest using a direct homing path (Fig. 6.14). And among these, preliminary experiments have confirmed that *S. niveimarginatus*, *A. triguttulus*, and *A. rotundus* use a visual compass-based path integration system for provisioning navigation, in addition to *P. japonensis* (Hironaka, unpublished

Fig. 6.14 Seed-provisioning subsocial bugs, *Adomerus triguttulus* (**a**), *A. variegatus* (**b**), *A. rotundus* (**c**) and *Canthophorus niveimarginatus* (**d**), oriented toward their nest after attaching a seed of their host plants to the tip of their proboscis

data). This strongly suggests that the path integration system using a compass and a distance meter is not the exclusive property of hymenopteran insects, but has evolved in a wide range of insect taxa. Even more interestingly, the remaining species, *S. cinctus*, appears to use a trail pheromone for provisioning navigation. Kight (1995) observed that *S. cinctus* females traced back along the outbound path with remarkable precision, even when parts of the return route involved movement away from the nest. However, there is no experimental evidence for the trail pheromone.

There are still many mysteries in the orientation and navigation abilities of *P. japonensis*, even at the behavioral level. For example, it is not at all clear about the distance meter that is required in addition to the compass in the path integration system. They may be using "odometers" in their legs like *Cataglyphis* ants (Wittlinger et al. 2006) or optic flow like honeybees (Esch and Burns 1996). The canopy compass is also a mystery. The forest canopies encountered by provisioning females of *P. japonensis* are complex and diverse. Instead of the simple structure artificially shown in our field experiment, the gaps in the canopy are fine and numerous. How does a provisioning female choose a gap as a reference point for its compass? The shape and size of the canopy gap will change significantly over long-distance provisioning trips and in some cases will disappear. The visible gap may be temporarily obscured by a tree trunk or other object during provisioning excursion and by wind. Canopy gaps are unstable compass markers, unlike celestial cues. How do bugs solve these problems? The unique orientation and navigation of *P. japonensis* in the forest still hold many fascinating secrets that await better understanding of the behavioral abilities in animal navigation.

6.3 Process Used by Females to Identify a "Good" Drupe

One of the most enjoyable studies carried out in the field took place in 1994 when we sought to understand how females were deciding which drupes to transport back to the nest. This study was truly fun!

As we have described, we regularly saw hundreds of drupes on the ground; when females were provisioning, they most often passed most drupes by without a glance. We wanted to clarify the cues that females were using to select the perfect drupe worthy of transport back to the nest to feed their hungry nymphs. As we have described in Sect. 4.3.1, on average, the drupes that females dragged back to their nests weighed from 1.7 to more than 5 times their body weight. They transported drupes at a formidable speed of over an average distance of 254 cm (range 160–430 cm) (Tsukamoto and Tojo 1992). We have not specifically assessed the cost of dragging one drupe back to the nest, but one can assume it is considerable both in terms of the energetics and the time involved. Nymphs will leave the nest prematurely if the female fails to provide sufficient food, so it behooves mothers to make the most of their provisioning efforts and only transport those drupes that are most nutritious back to their nest. To that end, natural selection should favor mothers who are able to carefully screen drupes and distinguish between those that are good and those that are of poor quality. During the provisioning season of 1994, we carried out a series of five field experiments to identify the cues that females were using to select "good" drupes (Nomakuchi et al. 1998).

First, we observed females provisioning in the field to see precisely what they were doing as they roamed around the foraging area and searched for a "good" drupe. In 1994, nests were distributed in a range of 5–15 m from the foraging area. Females began leaving their nests to provision from the third week of June, and provisioning behavior continued until early July. Hundreds of drupes were on the ground under the host trees. Females walked with their antennae in front of them waving about. They ignored most of the drupes around them, but occasionally a female stopped at a drupe, palpated it with the antennae, and grasped it with the front four legs. Then she rolled it around with those front four legs for a few seconds, keeping it under the abdomen. Next, the female inserted the proboscis into the drupe. The female repeatedly inserted and withdrew the proboscis from the drupe. This "tasting" behavior continued for about 10 s to several minutes, until the female either rejected the drupe by dropping it and walking away to inspect another drupe or accepted it by piercing it even further and hastily dragging it back to its nest (Nomakuchi et al. 1998).

Females were also seen directly competing over drupes. The competitive bouts proceeded as follows. After one female found a drupe, inspected it, determined it was "good" and was hastily returning to its nest, she would be intercepted by several other provisioning females, each trying to aggressively pull the drupe away from the others. On one such occasion, we saw eight females engaged in such a tug-of-war for 2 h! Eventually, a few females gave up and went off to forage in the traditional manner, but several clung to the drupe even as the victorious female was dragging it away! These competitive bouts were especially common when two drupes were connected to the same bit of stem and could be dragged off together. It seemed like the different movement of the female once a "good" drupe had been secured, switching from the stop and start movement and repeatedly changing direction to a beeline straight run in a very fast, continuous pace, clued other females to the fact that one of them had secured a "good" drupe and initiated the tugs-of-war. More on this curious behavior in Sect. 6.4!

6.3.1 Relationship Between Drupe Features and Acceptability to Provisioning Females

Drupes on the ground had an outer skin that varied in color, based on maturity of the drupe. Most were green (least ripe) or a bright cherry red, indicating that most drupes fall from the tree before they are ripe. As drupes matured, they became dark red. Some very ripe drupes were purple or black, and there were also drupes that had ripened to the point that their skin and the fleshy part of the drupe got washed away altogether. Those drupes were tan or whitish and much smaller. At the natural field site, we observed the rate at which provisioning females encountering each of the different colored drupes accepted or rejected them. Females accepted only about 35% of green drupes, but they accepted 71% of red drupes and 100% of dark red, purple, and skinless drupes (Fig. 6.15; Nomakuchi et al. 1998). They were clearly able to distinguish which drupes were most ripe.

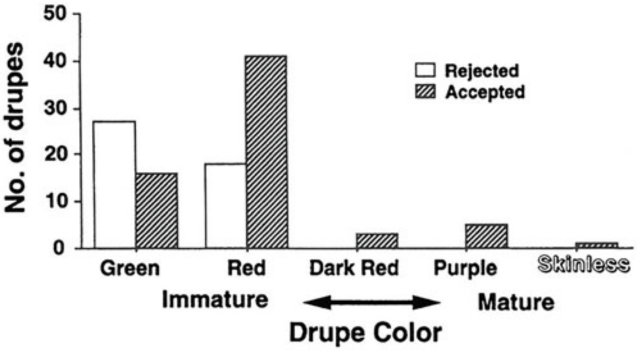


Fig. 6.15 Relationship between drupe color and acceptability to provisioning female *P. japonensis* in the field. Total drupes, $n = 97$. Adapted from Nomakuchi et al. (1998)

The drupes that females accepted were slightly, but significantly, larger than those that were rejected, probably because the outer skin thickens as the drupe matures until it falls off (Fig. 6.16a; Student's t test, $p < 0.04$; Nomakuchi et al. 1998). They were also significantly heavier (68%), likely reflecting a more developed dense endosperm (Fig. 6.16b; Student's t-test, $p < 0.002$).

Drupes are composed of an outer skin, an inner shell, a fibrous layer, and endosperm. As drupes mature, the fibrous layer is gradually converted to endosperm (Fig. 6.17; Nomakuchi et al. 1998). Apparently to develop their eggs inseminated females sequentially feed on many yellow and green drupes on the host tree that only have between 5 and <20% endosperm. After weighing and measuring the drupes, we split them open to estimate the endosperm content. The average endosperm content of accepted drupes was over four times greater (78%) than rejected drupes (Fig. 6.18; Nomakuchi et al. 1998), indicating that females can assess the amount of

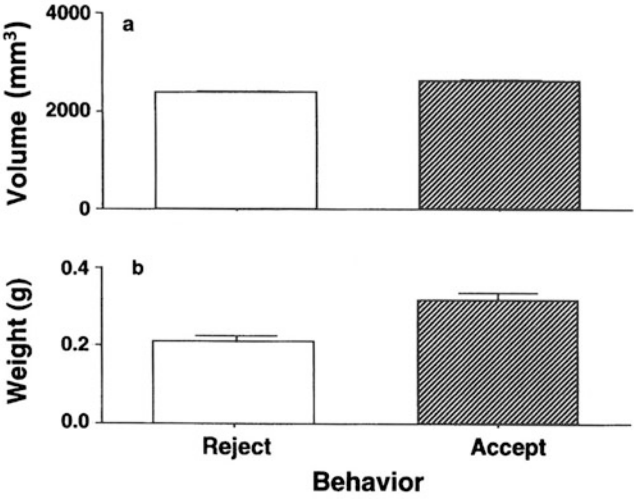
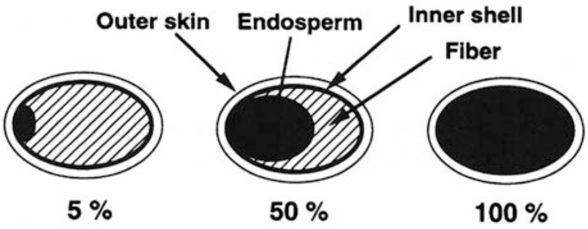


Fig. 6.16 Relationship between drupe volume and weight and acceptability to provisioning female *P. japonensis* in the field. Measurements done on 44 drupes that were rejected and 52 drupes that were accepted. Values represent means ± SE. (**a**) volume, Student's t-test, $p < 0.04$; (**b**) weight, $p < 0.002$. Adapted from Nomakuchi et al. (1998)

Fig. 6.17 Internal composition of drupes of different maturity. Fiber is gradually replaced with endosperm as the drupe matures. Adapted from Nomakuchi et al. (1998)



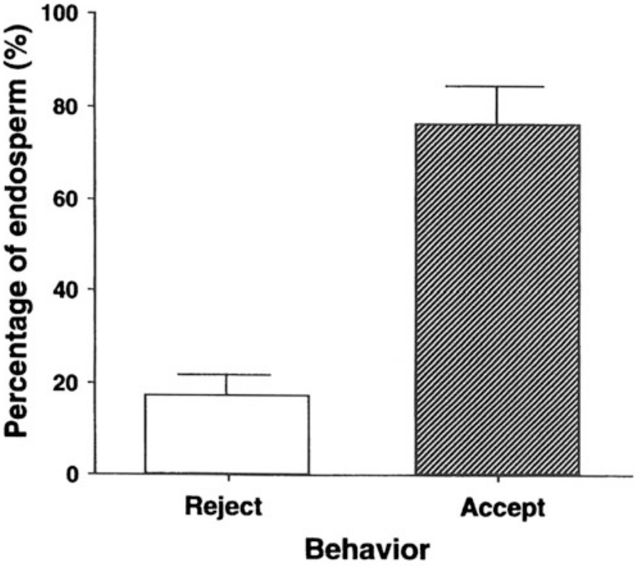


Fig. 6.18 Relationship between amount of endosperm in a drupe and acceptability to provisioning *P. japonensis* females in the field. Values represent mean ± SE. Mann-Whitney U test, $p < 0.0002$. Adapted from Nomakuchi et al. (1998)

endosperm inside a drupe and were primarily bringing "good" drupes back to the nest to feed their young. Now that we had verified that females were actually choosing drupes that were more mature and had higher endosperm content, we set out to identify the cues they were using to identify "good" drupes.

6.3.2 Initial Cues Used by Provisioning Females that Led to Approaching a Drupe

We carried out a choice test and a non-choice test in the field to determine whether females were using volatile cues or color when they decided to approach a drupe. We placed a Y tube in the field and put a green drupe in one short end and a red drupe in the other short end. The female was allowed to enter the long end and choose either of the drupes. Of ten trials, nine females chose the arm with the mature drupe. Moreover, when 15 females were exposed to a green drupe that had its skin cut, all of them approached the drupe, although before it had been cut, they ignored it completely (Nomakuchi et al. 1998)! These findings indicated that females use volatile cues to initially approach a drupe, not color; the volatiles in green drupes are probably in very low concentration and remained unrecognizable by females until the skin was broken.

6.3.3 Weight as a Possible Cue to Accept a Drupe

Although females approached the green drupes that had been cut, after probing them and grasping them in their four front legs, rolling them a bit, every female rejected them. So, what other cues were the females assessing to verify the quality of the drupe? We thought weight might be a factor. To test this, we peeled the skin off green drupes to release more volatiles that would attract the female and injected water into the drupes to make them heavier. We presented these weighted drupes to ten females. The females approached them, probed them with the proboscis, and rolled them around in their legs, but, alas, they did not accept them. So, something else must be the main cue.

6.3.4 Nonvolatile Juices in the Outer Skin as a Possible Cue to Accept a Drupe

We tested whether the taste of juices in the outer skin acted as a cue for acceptance of a drupe. We peeled the juicy skin off very ripe drupes and smeared the juice all over immature green drupes (13 trials) and wooden dummies that were about the size and shape of a drupe carved from untreated wooden branches from the forest floor (11 trials). Interestingly, all females approached, inspected, and dragged off the flavored substrates of both types (Nomakuchi et al. 1998). This indicates that females are tasting the drupes when they probe them, and the taste is determinant in whether they accept the drupe.

6.3.5 Consistency of Drupe as a Possible Cue for Its Acceptability

To clarify whether provisioning females recognized that the hard inner endosperm was the target, and not just the odorous and flavorful skin, in a choice test 17 provisioning females were presented with just the juicy skin of a mature drupe and a wooden dummy drupe encased in the skin of a mature drupe. All females approached both bait items, but only dragged off the fragrant skin-encased wooden dummy (Nomakuchi et al. 1998). This demonstrated that females require cues from the volatile chemicals, the taste, and the solid core.

6.3.6 Can Females Recognize Just the Endosperm with No Chemical Cues from the Outer Skin?

In a final choice test to determine whether females were able to recognize the final goal of their foraging efforts, the endosperm, in the absence of the attractive chemical cues, 34 provisioning females were presented with the fragrant juicy skin and inner shell of a mature drupe and a bare, mature endosperm whose outer skin was carefully removed such that no juices contacted it. Four females approached the endosperm, inspected it, and dragged it off. Two of 30 females that approached the skin and inner shell dragged the drupe off. Nine of the 28 females that rejected the skin accidentally came upon the endosperm, inspected it by probing and rolling it, and dragged it off. In other words, they did not extend and flagellate their antennae in the direction of the endosperm as if they were attracted to it, as they did with the fragrant skin. The remaining 19 females that had initially inspected the skin just wandered off and never came upon the endosperm (Nomakuchi et al. 1998). Clearly, it is difficult for provisioning females to find endosperm without the juices of the outer skin, stressing the importance of these chemical cues as an attractant to initially finding a good drupe. In the field, when a drupe matures to the point where the skin falls off, the inner shell remains and there would usually be dried juices on the outside of the endosperm that emit the fragrant, attractive volatile chemical cues, so there is no need for selection to have favored females that could recognize endosperm with no juice fragrance.

Finally, we compared the time it took from approach to acceptance of the bait for transport back to the nest of 11 females that had accepted a wooden dummy drupe encased in the skin of a mature drupe and 10 females that had accepted an endosperm. Females took significantly less time to inspect and accept the endosperm than the skin-encased wooden dummy drupe (Fig. 6.19; Mann-Whitney U test, $p < 0.01$; Nomakuchi et al. 1998). Females accepted the endosperm in about 1/6 the amount of time required for females to accept and transport to the nest a fragrant dummy drupe. The females apparently recognized that something was off but decided to risk the time and energy cost should it turn out not to be a good drupe and transported it to the nest.

6.3.7 Conclusions About Drupe Selection Process

We summarize the drupe selection process in Fig. 6.20 (Filippi et al. 2001). Females were most directly attracted to approach the bait when it had the fragrant odor of a mature drupe, but only accepted it if it also had the texture of a hard endosperm. They could recognize just the endosperm if they touched it by accident, but never approached it in the absence of the appropriate chemical cues.

The data demonstrate that females use reliable cues to distinguish good drupes from bad. They choose the most mature, heaviest, and largest drupes with high

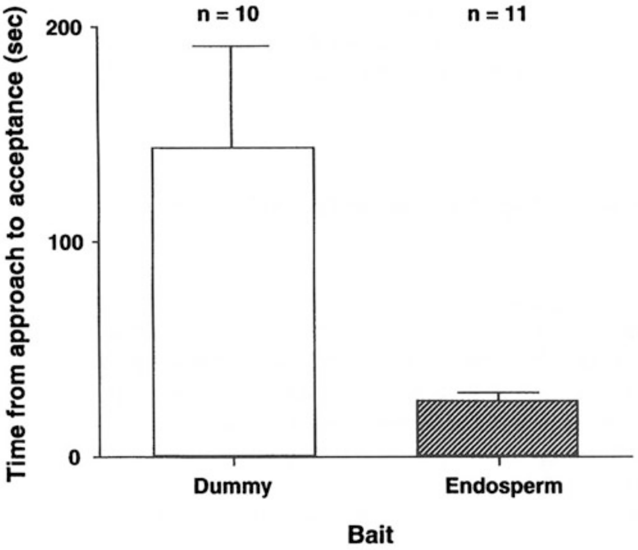


Fig. 6.19 Inspection time of provisioning *P. japonensis* females in the field when exposed to fragrant skin-encased wooden dummy and endosperm. Mann-Whitney U test, $p < 0.01$. Adapted from Nomakuchi et al. (1998)

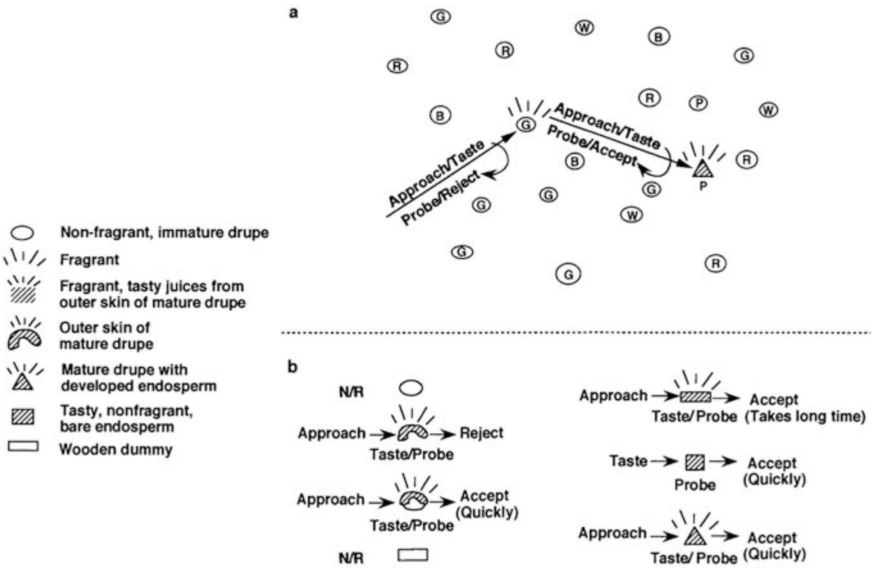


Fig. 6.20 Behaviors of provisioning female *P. japonensis* prior to accepting or rejecting a drupe. (**a**) Behaviors in response to natural drupes in the field; (**b**) Composition of manipulated and artificial drupes and female response. Adapted from Filippi et al. (2001)

percentages of endosperm (Figs. 6.15, 6.16, 6.17, and 6.18). They are attracted to and approach drupes in response to volatile and tactile chemical cues and accept them for transport to the nest if they also have a dense core that is assessed by weight and probably also by probing with the proboscis. Under natural conditions, these criteria are sufficient to ensure that females are selecting only good quality drupes to provision their nests.

6.4 Alternative Foraging Behavior: Kleptoparasitism

As alluded to in Sect. 4.19.5, females were sometimes seen removing drupes from the nests of other females, essentially usurping a resource that the resident female had invested considerable time and energy to procure. Depending on how commonly it occurs, this behavior, known as kleptoparasitism (Rothschild and Clay 1952; Brockmann and Barnard 1979; Iyengar 2008), could be quite costly to the resident female. A variety of selective pressures that can fluctuate widely promote the evolution of inter- and intraspecific stealing from another individual's diligently provisioned cache. The availability of the resource in both quantity and quality (Nilsson and Brönmark 1999), density of intraspecific or interspecific competitors (Scott 1994), and the tendency for host nests with stored food to be aggregated (Elgar 1988) can drive the evolution of kleptoparasitism. Increased density of foragers combined with increased handling time of the resource leads to increased rates of kleptoparasitism (Brockmann and Barnard 1979). However, while the motivation of kleptoparasites to steal from a particular individual will be affected by these selective pressures, the age (Tso and Severinghaus 1998), condition, and response of the host (Elgar 1988; Cangialosi 1991) will play a big role in determining the success of a kleptoparasitic event for the parasite and the cost to the host. Because of the likely fluctuation in all these parameters, risk-sensitive behaviors should be adopted by both the parasite, to enhance the likelihood of success, and the host, to minimize the cost.

Risk-sensitive behavior, primarily in response to food availability, was shown to occur with regard to trophic egg production (Filippi et al. 2012) and nest site preference (Filippi et al. 2002) in *P. japonensis*. When one considers the severe constraints imposed by the unpredictable and poor resource (Nomakuchi et al. 1998; Filippi et al. 2002) that have favored the evolution of such extensive and unusual parental care behaviors, including progressive provisioning, and extreme physiological adaptations (Tojo et al. 2005; Kashima et al. 2006; Hosokawa et al. 2012, 2013) and add on the further limitation of obligative semelparity, it is not at all remarkable that stealing to procure the precious resource should also occur in this eclectic species. In fact, provisioning females would be expected to assess the likelihood of finding a good drupe and use risk-sensitive decision-making to choose a foraging strategy that is most likely to meet with success. If search time is extraordinarily long, and a provisioning female comes upon either another female who has secured a good drupe and is returning to its nest or a nest that has been provisioned with many good drupes, stealing should be the optimal behavior. In other words, when the payoff from stealing exceeds that from self-foraging, provisioning females should opt for kleptoparasitism (Brockmann and Barnard 1979; Broom and Ruxton 1998; Flower et al. 2013). We set out to determine how common kleptoparasitism is in *P. japonensis* and to test the hypothesis that the prevalence for nest sites that are outside the foraging area is associated with reduced risk of kleptoparasitism. We predicted that females nesting within the foraging area would suffer a higher rate of kleptoparasitism and lower success overall up to the time of nest abandonment because their nests would be physically more exposed to predators and to kleptoparasitism because of sparse leaf litter and protective vegetation (Tsukamoto and Tojo 1992); the higher density of foraging females inside the foraging area should also lead to more opportunistic thievery there than outside the foraging area (Filippi et al. 2002).

We carried out a manipulated field study during the provisioning season of 2000 (June and July) at our field site at Mt. Hinokuma Park in Saga, Japan. Three clustered large host trees, the crowns of which largely overlap, serve as the resource for the subpopulation at this site. The foraging area encompasses the area under the overlapping crowns and slightly downhill of the trees where the fallen drupes roll. The radius from the center of the three trees to the edge of the foraging area is about 3.5 m and is relatively bare of ground cover. On the other hand, just outside this area, where most females tend to nest, the ground is covered with abundant leaf litter and vegetation. We searched for nesting females inside and outside the foraging area, but at this site in 2000, nesting females were only found outside the foraging area. We collected 32 females and re-established their nests, preparing 16 nests inside and 16 nests outside the foraging area. We set each egg mass-bearing female into a small depression in the soil and covered the nest with leaf litter. To prevent predator disruption to the nests prior to hatch, we enclosed each nest in a polypropylene cylinder (10 cm diameter, 15 cm height) sealed with a plastic bag and sprayed water on the nest daily. We carefully inspected the nests daily, and upon hatch, the cylinders were removed so the females could forage freely. The inside nests were about 1.5 m from the edge of the foraging area, and the outside nests were about 1.5 m outside the edge of the foraging area (Fig. 6.21; Filippi et al. 2005). Because the amount of energetic reserves a female entered the provisioning season with would affect her provisioning capacity, we measured an initial female energy index (body weight <g>/pronotum width <mm> of all females). There was no significant difference between females in the two groups. The parameters assessed throughout the provisioning season included incidence of kleptoparasitism (fewer drupes at inspection than at the previous inspection), number of drupes provisioned, female vigilance (presence of female in the nest when inspected), development rate and survivorship of young, persistence of nest, and resource pressure (good drupes/female, described in detail in Sects. 4.19.2 and 4.19.3).

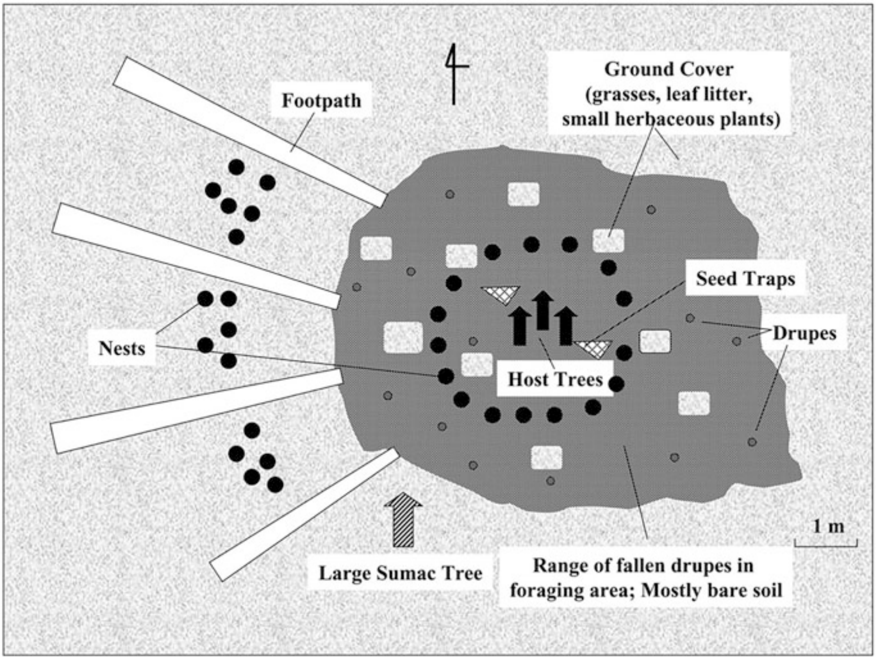


Fig. 6.21 The manipulated field site at Mt. Hinokuma in Kanzaki Town, Saga, Japan, in 2000. Nests were established inside (darkly shaded area around the host trees) and outside the foraging area. Lightly shaded areas represent ground cover (grass, leaf litter, herbaceous plants, etc.), which was sparse inside the foraging area. Adapted from Filippi et al. (2005)

6.4.1 Factors Related to Rate of Kleptoparasitism

Interestingly, both inside and outside nests suffered approximately equal rates of kleptoparasitism; however, though the difference was not quite significant and consistent with our prediction, inside nests had nearly twice as many drupes removed from them as outside nests (Table 6.1). The values in the table for stolen drupes are also most likely very conservative, because, to minimize disturbance, we only checked the nests every other day. It is possible, and even likely, that many

Table 6.1 Conditions within nests inside and outside the foraging area

	Inside ($n = 16$)	Outside ($n = 16$)	Mann-Whitney U test: $P =$
No. kleptoparasitized nests	14/16	13/16	NS
Mean no. drupes stolen (± SE)	4.0 ± 0.72	2.2 ± 0.56	0.06
Mean final no. drupes provided (± SE)	13.9 ± 2.5	6.5 ± 2.0	0.025
Female presence/absence in nest	50/78	42/92	NS

Adapted from Filippi et al. (2005)

more drupes during unobserved times had been provisioned and then stolen. Females tended to remember a good site and return to it repeatedly.

The resource pressure in 2000, calculated using the method in Table 4.7, revealed that the FDI was extremely low (i.e., high resource pressure) in 2000 (0.29) and very similar to that in 1998 (0.28), as was the provisioning capacity. Interestingly, no females were found nesting inside the foraging area early in the season that year either.

Pattern of Drupe Availability

Despite the greater number of drupes stolen from inside nests, provisioning by inside females increased steadily throughout the critical third stadium. On the other hand, provisioning by outside females increased at a much slower rate than inside females and, in fact, plateaued during the middle of the still very vulnerable second stadium (Fig. 6.22; Filippi et al. 2005). We waited until all nests had been abandoned before counting the final number of drupes available to nymphs. Surprisingly, despite the higher rate of kleptoparasitism, in the end, inside females still provisioned significantly more drupes than outside females (Table 6.1)! It is noteworthy that even

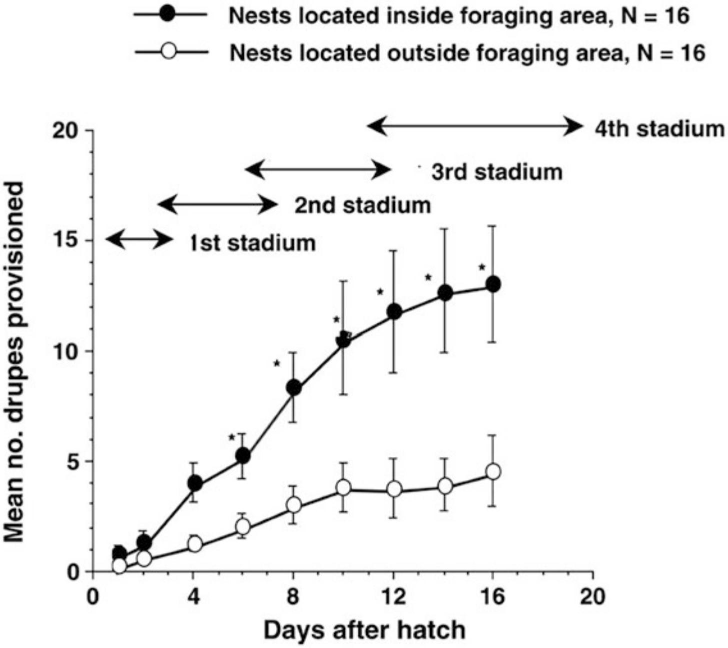


Fig. 6.22 Relationship between nest location and provisioning capacity of females throughout the provisioning season of 2000. Error bars represent S.E. *Mann-Whitney U test, $p < 0.05$. Adapted from Filippi et al. (2005)

though inside females ultimately provided more than twice as many drupes as outside females, the average number was still among the lowest we have seen over the years (Filippi et al. 2002), reflecting the very poor resource availability in 2000.

We expected that those females able to find drupes more easily would spend more time guarding nymphs in the nest. However, while females were present in the nest at 54% of the observations in the inside nests and 46% of the time in the outside nests, at this sample size the difference was not significant (Table 6.1). The extremely low number of good drupes in 2000 probably required that all females spend as much time as possible foraging.

6.4.2 Effect of Energetic Reserves on Provisioning Capacity

We found no significant relationship between energetic reserves and the final number of drupes provisioned by inside females; however, this was not the case with outside females. There was a significant positive correlation between energetic reserves and the final number of drupes provisioned by outside females (Bartlett $\chi 2$, $p = 0.027$). Recall that no females had prepared nest sites within the foraging area in 2000; we randomly *assigned* the females we collected from their chosen nest sites outside the foraging area to nest sites inside and outside of the foraging area. Because none had actually chosen either of those sites, it is possible this finding is an artifact of the experimental design. Also, we suspect that the inside nests prepared by us had better litter cover than would normally occur within the foraging area, and that could have made it safer for inside females and their nests than if the nests were completely natural. This finding bears further scrutiny under more natural nesting preference conditions.

6.4.3 Development and Survival Rates of Nymphs Inside and Outside the Foraging Area

Nymphs in inside nests developed significantly faster than those in outside nests (Fig. 6.23; Filippi et al. 2005). The stage of development was significantly advanced for nymphs in inside nests by day 4, and the numbers of nymphs in outside nests dropped off dramatically by day 6 (Fig. 6.23). Survivorship was also dramatically lower for outside nests (Fig. 6.24; Filippi et al. 2005). In fact, outside nests had lower survivorship than inside nests from the first day of observation and showed a sharp decrease in survivorship of 37% between days 4 and 6, while inside nests showed a much more gradual decline and leveled off at 40% by day 10. Survivorship of outside nymphs had dropped to about 10% by day 10. These findings of lower success in outside nests surprised us as over the years females have shown a clear preference for nesting outside the foraging area (Filippi et al. 2002). Why would

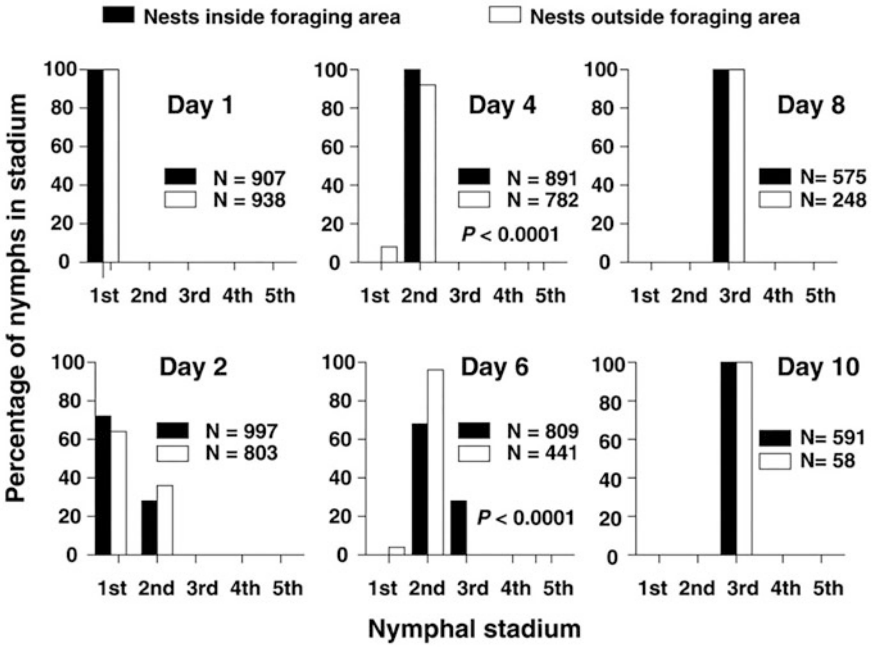


Fig. 6.23 Effect of nest location on development rate of nymphs. Adapted from Filippi et al. (2005)

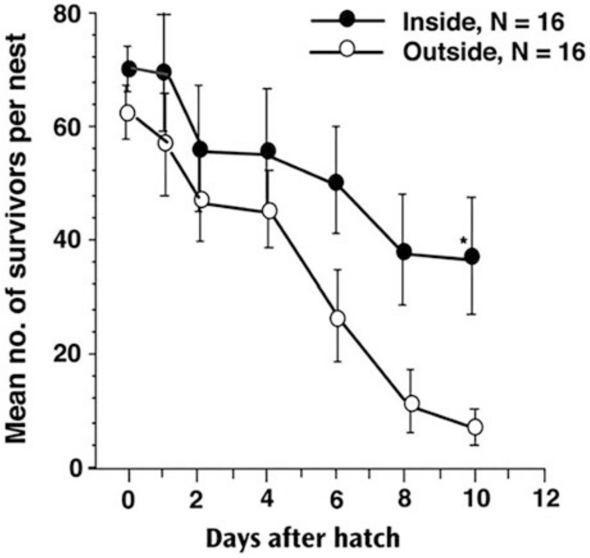


Fig. 6.24 Relationship between nest location and survivorship of *P. japonensis* nymphs. Survival curves plotted by Cutler-Ederer method. Error bars represent S.E. Mann-Whitney U test, $p = 0.02$. Adapted from Filippi et al. (2005)

there be such a clear preference for nesting outside the foraging area if the inside nesters do better? We consider this in Sect. 6.4.5.

6.4.4 *Persistence of Nests Inside and Outside the Foraging Area*

Initially, and as predicted (finally!), the number of intact nests was slightly higher than that of inside nests. However, by day 6 the pattern was reversed, and, contrary to our prediction once again, by day 8 the difference was significant with twice as many inside nests as outside nests remaining intact (Fig. 6.25; Filippi et al. 2005). It is highly likely the very poor provisioning capacity of the outside females leads to early departure of the nymphs from the nest.

6.4.5 *Conclusions of This Study*

So what did we learn through this study? Well, we certainly discovered that kleptoparasitism is not a rare behavior at all in this species but is in fact quite widespread (Table 6.1), at the very least under the resource conditions of 2000 at this particular site. We don't know if it is as common every year as it was in 2000,

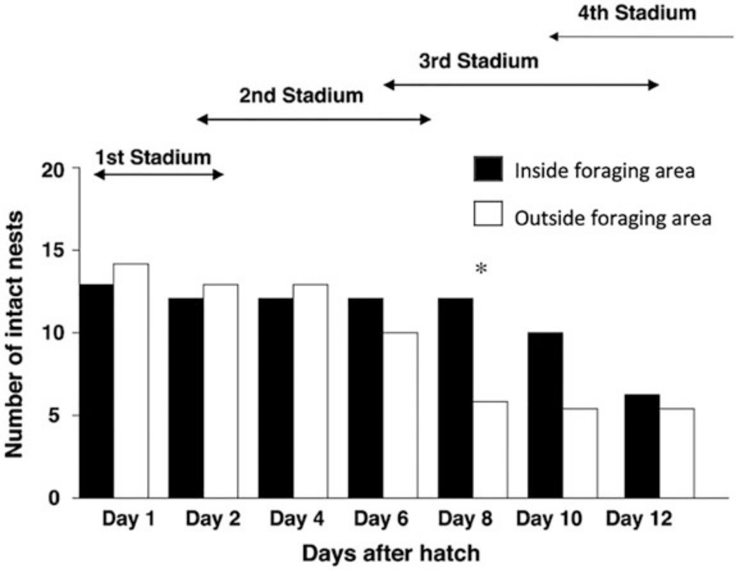


Fig. 6.25 Persistence of nests inside and outside the foraging area during the nesting stage. Adapted from Filippi et al. (2005)

but with the extremely poor resource conditions that year, almost all nests had experienced some kleptoparasitism. We were also humbled by the number of our predictions that turned out to be wrong. However, never to be discouraged, we attribute several of our miscalculations to our keen desire to make sure the inside nests did not disappear so early in the study that we would have been unable to collect any data at all. In hindsight, the inside nests were far better protected with leaf litter than they would have been under natural circumstances, which is likely why no females were nesting there to begin with! Moreover, the biggest factor that every field ecologist must always contend with when interpreting results of field studies is, of course, the fact that there are invariably multiple ecological conditions that are beyond our control and that very likely affect the results of our studies in different ways in different years. For example, we could not have predicted the very poor resource this year, which surely affected the outcome of our study. But what we can do is incorporate as many of the relevant factors that we encountered into our interpretation of the results. And we can only EVER say that the results of our study apply to the conditions at this particular site in this particular year. Even within our small Mt. Hinokuma, there were at least 59 subpopulations at the time of this study, and the ecological conditions, including resource abundance, varied considerably from site to site.

So, it seems that when the resource pressure is as severe as it was at this site in 2000, females nesting outside the foraging area (where we found them nesting initially) have very poor success (Figs. 6.23, 6.24, and 6.25). We concluded that the combination of travel time to and from the foraging area and the extreme scarcity of good drupes (increased handling time) was devastating to the success of outside females that season. Such conditions would increase the benefit of the stealing strategy (Hockey and Steele 1990). However, there are trade-offs involved and costs and benefits associated with each tactic, and at this point in our research we were unclear whether stealing was limited to opportunistic encounters or whether it had evolved as an alternative foraging tactic. At any rate, a decision to steal or self-forage will depend on a variety of factors, and the range of options extends from self-foraging only to stealing only; there will come a point where the costs of sticking to one tactic outweigh the benefits and a switch will occur (Broom and Ruxton 1998). Risk-sensitive decision-making would mitigate the economic costs involved such that each option would be chosen when the payoff associated with it outweighs the costs (Brockmann and Barnard 1979; Broom and Ruxton 1998; Koops and Giraldeau 1996; Flower et al. 2013). Having the plasticity to respond to the ecological conditions encountered is the key to success.

For the host, the costs of stealing are obvious, but what might be the cost to the kleptoparasite? Mantaro Hironaka observed behaviors during this study that suggested stealing from a nest was not without cost, at least when the host female is present. Host females were seen aggressively engaging with the would-be kleptoparasite, and so began our quest to answer another series of questions regarding the evolution of strategies by the host to counter the costs of kleptoparasitism.

6.5 Guarding Behavior Against Intraspecific Kleptoparasites

Kleptoparasitism of food that a parent has invested energy into procuring can occur outside the nest, along the route back to the nest with the food item, or inside the nest after the provision has been deposited (Field 1989a, b, 1992; Villalobos and Shelly 1996). Similar to what has been reported for solitary wasps (Field 1989a, b, 1992; Villalobos and Shelly 1996; Kurczewski and Spofford 1998), provisioning *P. japonensis* females who have succeeded in finding a drupe are often accosted by other foraging females on their way back to the nest, and lengthy tugs-of-war and grappling over the prized drupe may ensue (Filippi-Tsukamoto et al. 1995; Filippi et al. 2002). Because the loss of provisions that were acquired at great cost could severely impact a female's fitness, natural selection should favor the evolution of strategies that would mitigate the risk of kleptoparasitism. Reports of defensive behavior against kleptoparasitism are scarce, but brooding females of the dung beetle *Copris lunaris* aggressively defend dung balls against potential thieves (Klemperer 1982; Costa 2006). We undertook a study to investigate the effectiveness of guarding and defensive strategies against kleptoparasitism in *P. japonensis*.

6.5.1 Guarding Behaviors Displayed

During the provisioning season (June and July) of 2000, we set out to identify whether females could effectively mitigate the threat of intraspecific kleptoparasitism. We hypothesized that there would be specific and effective defensive behaviors against intraspecific kleptoparasites. To verify the resident female in a nest, we marked the elytra of 67 egg-guarding females and labeled the nests with our regular trusted chopstick flags. Once the provisioning season got underway, when we located a marked female foraging for a drupe, we set a "good" drupe in front of her. The female took up the drupe and dragged it back to her nest. We gently removed the leaf litter to observe what was happening in the nest, specifically the female's behavior, the stage of nymphal development, and the nymphs' behavior. After depositing the drupe in the nest, the female remained holding the drupe for a time as the nymphs gathered on it. We called this the holding phase (Fig. 6.26a). The duration of the holding phase decreased significantly with progression of the nymphal stadia (Fig. 6.27; two-way ANOVA, $p < 0.001$). The holding phase could clearly be distinguished from feeding because the proboscis remained still rather than moving up and down as is seen during feeding. After the holding phase, the female shifted off the drupe and remained beside it and the feeding nymphs. We called this behavior the attending phase (Fig. 6.26b). Once a female initiated the attending phase for a newly deposited drupe, she never reverted to the holding phase.

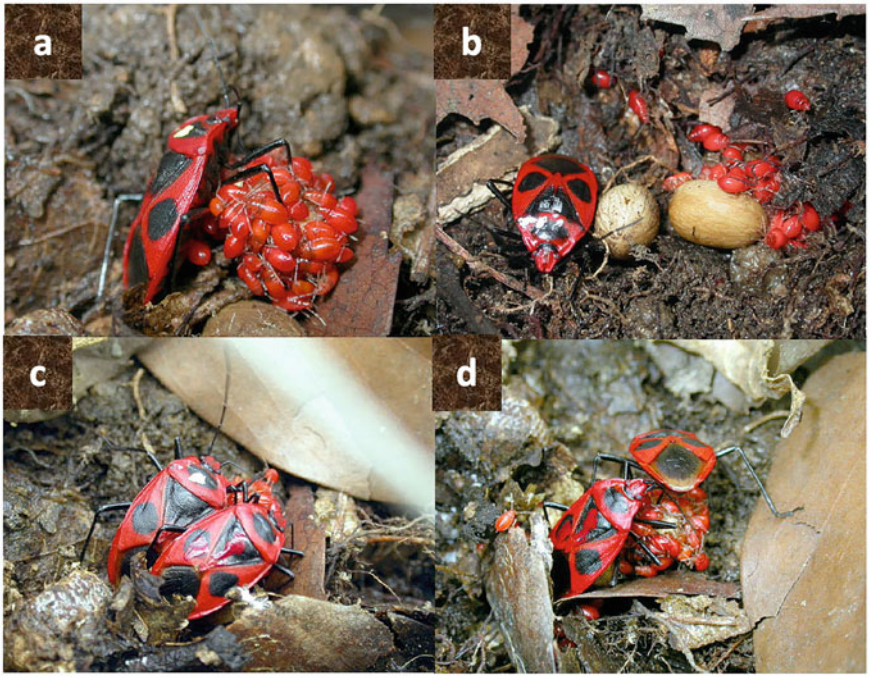
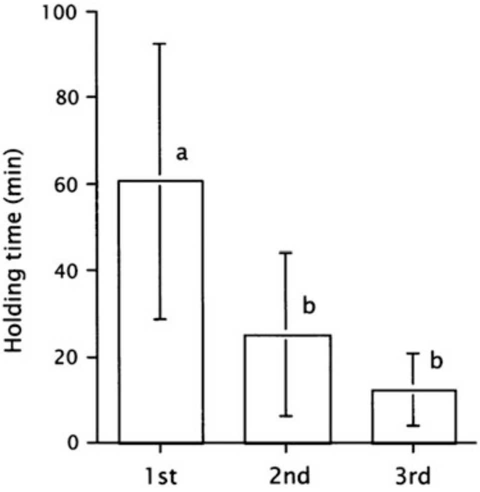


Fig. 6.26 Guarding behaviors displayed by resident *P. japonensis* females in the nest. (**a**) Typical holding behavior. The female that just returned to the nest with a drupe is holding the drupe, which is covered by a cluster of nymphs; (**b**) typical attending behavior; (**c**) resident female blocking intruder from gaining access to drupe; (**d**) resident female kicking intruder with hind legs. Adapted from Hironaka et al. (2008b)

Fig. 6.27 Female holding time for each nymphal stage. $N = 20$ for each stage. Error bars indicate S.E. Different letters above bars indicate significant difference (Scheffe's F test at $p < 0.05$). Significant decrease as developmental stage progressed (two-way ANOVA, $p < 0.0001$). Adapted from Hironaka et al. (2008b)



6.5.2 Effectiveness of Guarding Behavior Against Intruders

To observe the effectiveness of these behaviors against intraspecific kleptoparasites, 5 min after initiation of the holding phase, we carefully placed another foraging female right next to the entrance of the resident female's nest. The intruding female immediately entered the nest and attempted to remove the drupe. We observed the response of the 20 resident females to an intruder during the holding phase. Females displayed either no response or one or both of two different guarding behaviors in response to different levels of threat from an intruding female (Fig. 6.28). Upon contact with the antennae of the intruding female, the resident female, still holding the drupe, waved its antennae rapidly and emitted a soft chattering sound. The intruder attempted to insert its proboscis in the drupe and steal it, but the resident female (still in the holding phase) guarded the drupe by presenting its dorsum to the intruder, much like a shield, and attempted to push the intruder away (Fig. 6.26c). The resident female also sometimes kicked at the intruder (Fig. 6.26d). The altercation continued for up to 10 min and ended when the intruder either successfully

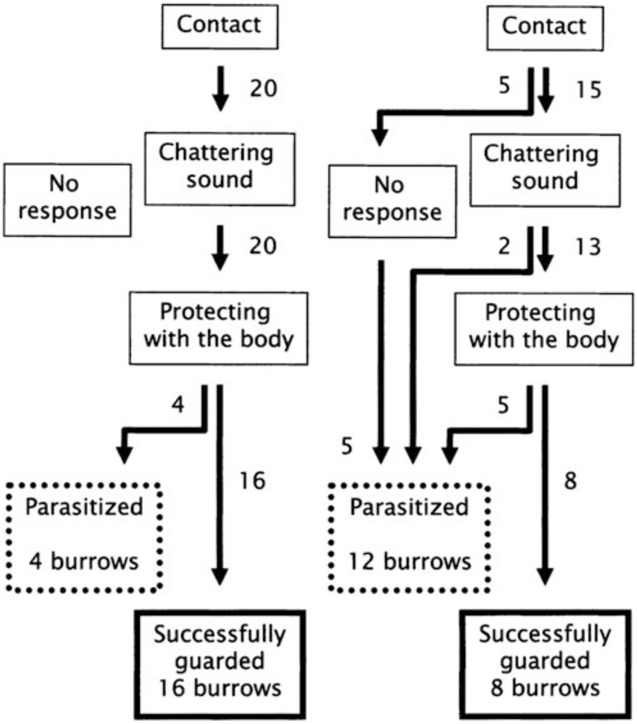


Fig. 6.28 Kinematic diagrams of guarding behaviors displayed against an intraspecific kleptoparasite. (**a**) behaviors displayed during the holding phase; (**b**) behaviors displayed during the attending phase. Numbers represent number of times behavior was observed. 20 burrows were observed in each phase. Adapted from Hironaka et al. (2008b)

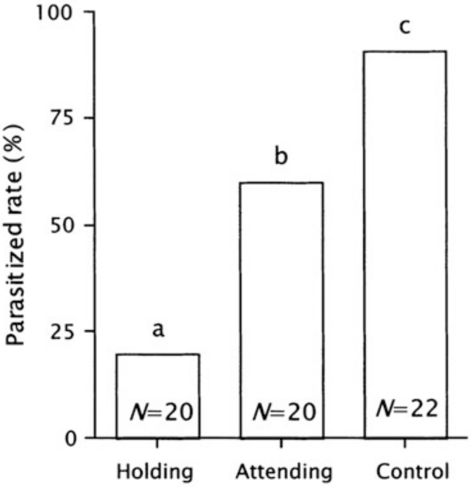


Fig. 6.29 Effectiveness of guarding phases as defense against intraspecific kleptoparasitism. Fisher's exact test, $p = 0.0128$. Control nests had female removed after nests were provisioned. Adapted from Hironaka et al. (2008b)

snatched the drupe and scampered off or relinquished its attempt to steal the drupe and left in defeat.

On the other hand, when we set a foraging female at the entrance to the nest 5 min into the attending phase, the response of the resident female was very subtle, with five attending females showing no observable response at all (Fig. 6.28). When the female was prevented from returning to her well-provisioned nest, ~90% of the nests were parasitized and nearly all the provisioned drupes were stolen (control group, $n = 22$; Fig. 6.29). Nevertheless, females in both the holding and attending phases demonstrated some success at defending drupes from thievery compared to the control group. However, behaviors displayed during the holding phase were significantly more effective at mitigating kleptoparasitism. Only 20% of nests were successfully parasitized during the holding phase ($n = 20$), while fully 60% of nests in the attending phase were parasitized (n = 20).

6.5.3 Summary of Guarding Behavior

The hypothesis that *P. japonensis* females display guarding behaviors to effectively reduce kleptoparasitism was supported (Figs. 6.26, 6.27, 6.28, and 6.29). We have demonstrated that kleptoparasitism occurs as an alternative strategy for foraging females to provision their nests (Filippi and Nomakuchi 2016; this work, Sect. 6.4). Nests of the solitary wasps discussed above and those of *P. japonensis* are spatially clumped, a condition that favors the evolution of kleptoparasitism (Eickwort 1975). It is, thus, reasonable that defensive behaviors to thwart the thievery should also evolve. When a female of one of these species that has finally procured food is accosted on its way back to the nest, the tugs-of-war and grappling behaviors ensue. If accosted just outside the nest, the female rushes into the nest with the food (Filippi-

Tsukamoto et al. 1995; Villalobos and Shelly 1996; Kurczewski and Spofford 1998; Filippi et al. 2002). The entrances to spatially clumped nests tend to be inconspicuous, and such is the case with *P. japonensis.* The female slips under a leaf that looks like any other leaf but is in fact the entrance to the nest (Tsukamoto and Tojo 1992). Hiding the entrance to the nest each time the female leaves is a strategy used by some wasps (Villalobos and Shelly 1996; Kurczewski and Spofford 1998). To minimize the risk of kleptoparasitism, female *P. japonensis* prefer to nest outside the foraging area, which has less protective leaf litter (Filippi-Tsukamoto et al. 1995).

Because the constraints on the different species vary, so will the particulars of the defensive behaviors. Being constrained to semelparity, *P. japonensis* has more to lose than the iteroparous solitary wasps who tend multiple nests at a given time. The wasps return to a nest, drop off the food, and leave to get more. Once sufficient food is provisioned, the mother does not return to the nest again (Villalobos and Shelly 1996). On the other hand, until they die from exhaustion, *P. japonensis* females divide their time between guarding the nest and provisioning. Searching time for drupes can take more than 2 h, so females often return to the nest intermittently even if they have not found a drupe and spend some time guarding the nest against predation and kleptoparasitism (Filippi et al. 2005; Hironaka et al. 2007a, b, c). Thus, females are faced with a precarious balancing act that involves splitting their time between the arduous task of searching for the essential food and mitigating theft of that precious resource by females intruding into an undefended nest.

While both phases of guarding behavior by *P. japonensis* females were significantly more effective at reducing theft of drupes than no behavior, the behaviors during the holding phase were much more effective than those during the attending phase (Fig. 6.26; Hironaka et al. 2007a, b, c). Why is this phase such an effective deterrent to kleptoparasitism? This seems to be related to the time-consuming series of behaviors that females engage in when searching for a drupe (Nomakuchi et al. 1998). The intruding female will first approach the drupe in response to the volatile chemicals it emits. Then she must pierce the skin and probe the drupe repeatedly to assess that it has a solid endosperm and that it tastes right. Then she must grasp the drupe with her fore- and mid-legs and roll it around to assess the weight. The posture and behaviors exhibited by the resident female during the holding phase essentially make the drupe inaccessible to inspection by the intruding female, who most often eventually gives up and leaves.

If the holding phase is so effective, why then do females release the drupe and move off to the side for the attending phase? Behavior of the voracious nymphs could shed some light on this, and it can also help us to understand why the duration of the holding phase goes from an average of 60 min during the first nymphal stadium to just over 10 min during the third stadium (Fig. 6.27). Nymphs gather on the drupe that the female has brought into the nest, but some also gather on the female and attempt to insert their proboscis through her exoskeleton to feed on her! We observed nymphs feeding on their mother inside the nest on four occasions; in three cases the diners were third instars, and in the remaining case they were fourth instars. It likely happens much more than that, and the older the nymphs, the more likely they are to attempt to feed on the mother. Clearly, the mother has another trade-off to deal with: the decision about how long to remain in the very effective holding phase and possibly become the victim of premature cannibalism, which would, of course, result in no more provisioning, and when to let go of the drupe, spending a few minutes attending and living to provision another day!

The nymphs are feeding while the female is holding the drupe, and the longer she holds it, preventing an intruding female from stealing it, the more they can feed. It is also very possible that the reason the female is holding the drupe is because she is secreting an enzyme to aid in digestion of the endosperm by the nymphs. This hypothesis requires further exploration; however, it would be compatible with providing time for the young to feed on the drupe before an intruder can steal it. It is also possible that a drupe that has been fed on by nymphs for the duration of the holding time might be unacceptable to intruding females.

6.6 Kleptoparasitism: An Opportunistic Behavior or an Evolved Alternative Tactic?

Intraspecific kleptoparasitism is widespread across taxa and among vertebrates has been reported in mammals, birds, reptiles, and amphibians. Among invertebrates, it has been documented in insects and spiders (reviewed in Iyengar 2008). Because the victim loses the resource, along with the energy invested to procure it, and the thief stands to gain considerably because the cost of searching is eliminated, the consequences of kleptoparasitism can have profound evolutionary implications (Brockmann and Barnard 1979; Iyengar 2008). The majority of examples of kleptoparasitism represent facultative and even opportunistic behavior. An individual happens upon another individual transporting the desired food item and, because the interloper is looking for food and has found it (the fact that another individual found it first is irrelevant), it tries to claim it. Representing the other end of the spectrum, cases of obligatory kleptoparasitism have also been identified (Brockmann and Barnard 1979; Field 1989a, b, 1992). In between these two extremes lies the condition whereby kleptoparasitism has evolved as an alternative tactic within a larger foraging strategy. The success of a kleptoparasitic tactic could have important consequences on the fitness of both the victim and the thief.

Parastrachia japonensis is severely constrained by an unpredictable and scarce resource, drupes of the host tree *Schoepfia jasminodora* (Filippi-Tsukamoto et al. 1995; Filippi et al. 2002). Their numbers are sporadic, and the quality of the drupes is very inconsistent and most often unacceptable to provisioning females. Because of these conditions, the search and handling time for the precious resource is extremely lengthy. Females can search for up to 2 h before finding a drupe worthy of inspection and then invest several minutes exposed to conspecific foragers and to predators while they inspect each drupe to make sure it is of high quality (Filippi-Tsukamoto et al. 1995; Nomakuchi et al. 1998). Lengthy handling times leave the foraging female vulnerable to exploitation by kleptoparasites (Sivinski et al. 1999). Foraging females steal from females in the process of inspection or soon after the drupe has been accepted and the female is heading off with it in haste (Filippi-Tsukamoto et al. 1995l Filippi et al. 2005). We suspect the hasty return to the nest with the drupe in tow, a very different movement pattern from the many other foraging females in the area engaged in a stop and start tentative inspection of drupes, serves as a cue to foraging females that a high-quality drupe has been procured. We once observed eight females engaged in a tug-of-war over a drupe that lasted for at least 2 h (Fig. 6.30; Filippi and Nomakuchi 2016). We consider this type of stealing to be opportunistic, although the ability to recognize the cue that a good drupe had been found must have evolved.

It is of interest to clarify the proximal mechanisms that could facilitate the evolution of kleptoparasitic behaviors. We considered that the behavior of entering a conspecific female's nest to steal a drupe seemed to be more deliberate than the opportunistic behavior of stealing from a foraging female. Thus, we tested the hypothesis that stealing from a nest was, indeed, evolved an alternative tactic to self-foraging that provisioning females use to provide high-quality drupes to offspring. In support of this hypothesis, we predicted that females would (1) be actively attracted to the nests of conspecific females and (2) that they would deliberately enter the nests to steal high-quality drupes.

Fig. 6.30 Eight females engaged in a tug-of-war over a prized "good" drupe. This went on for over 2 h. Arrows indicate other unacceptable drupes in the image. Adapted from Filippi and Nomakuchi (2016)

From June 3 to 10, 2008, we collected egg-guarding females with their original nest substrate of leaf litter and soil from the field site described previously and maintained them individually in the laboratory in lidded, clear plastic cups (8 cm d, 4 cm h) at 25 °C and a photoregime of 16L:8D. Within 24 h of hatch, the nest cups were transferred to an experimental arena designed as follows (Fig. 6.31; Filippi and Nomakuchi 2016). A clear plexiglass box was constructed (35 × 18 × 15 cm, L × W × H) with a plexiglass/mesh lid. The bottom of the box was layered with 5 cm of soil and sparse leaf litter. A hole large enough to accommodate a nest cup was dug 1 cm from either end of the box. Thus, when the nest cups were set into the soil in the box, the tops of the cups were flush with the soil and leaf litter so that the females could enter and leave their nests freely. The test female's nest was set at one end of the box, and an experimental nest was set at the other end. Unless otherwise stated, none of the test females had experienced provisioning prior to the trial. To avoid confounding effects from female interactions, the experimental nest did not have a female.

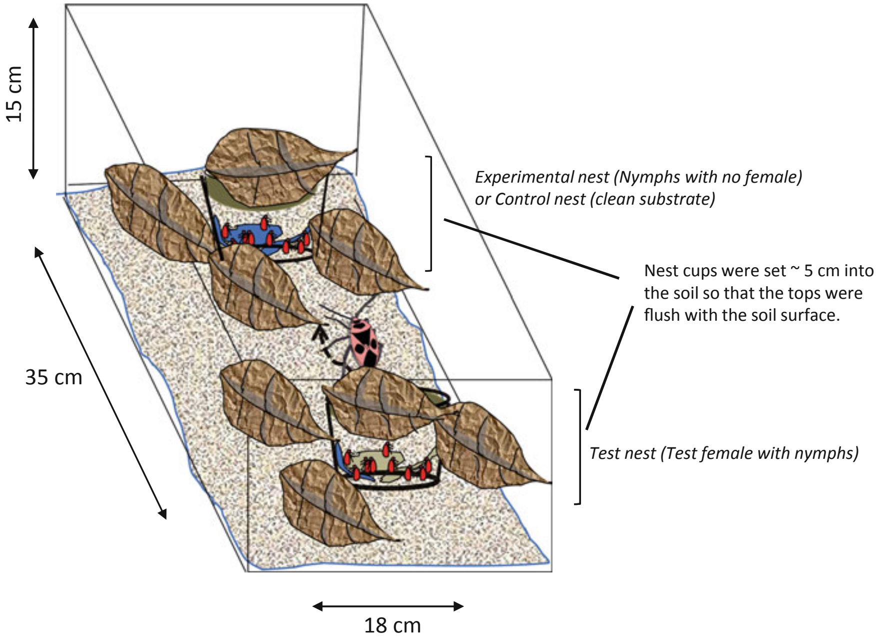


Fig. 6.31 Experimental arena. Test female with nymphs and original nest substrate (soil and leaf litter) in clear plastic cup in foreground; experimental nest (nymphs with nest substrate but no female) or control nest (clean substrate) in clear plastic cup at opposite end of plexiglass container. The bottom of the container was covered with 5 cm of soil and sparse leaf litter. Nest cups were set into the soil. The female could enter and leave nest freely. Adapted from Filippi and Nomakuchi (2016)

6.6.1 Are Females Attracted to Other Female's Nests?

To determine whether females were actively attracted to conspecific nests, the "other" nest was either an experimental nest containing the nymphs and substrate of a conspecific nest ($n = 12$) or a nest cup containing control substrate (clean substrate with no nymphs; $n = 12$). After removing the lid of the test nest, the test female could leave her nest to forage. We counted the number of females that entered the experimental and the control nest. Eight times as many females entered the experimental nest containing nymphs and substrate of a conspecific nest, compared to the cup with the clean substrate (Fig. 6.32a; Fisher's Exact Test, $p < 0.005$; Filippi and Nomakuchi 2016). Females were significantly more attracted to conspecific nests compared to control nests.

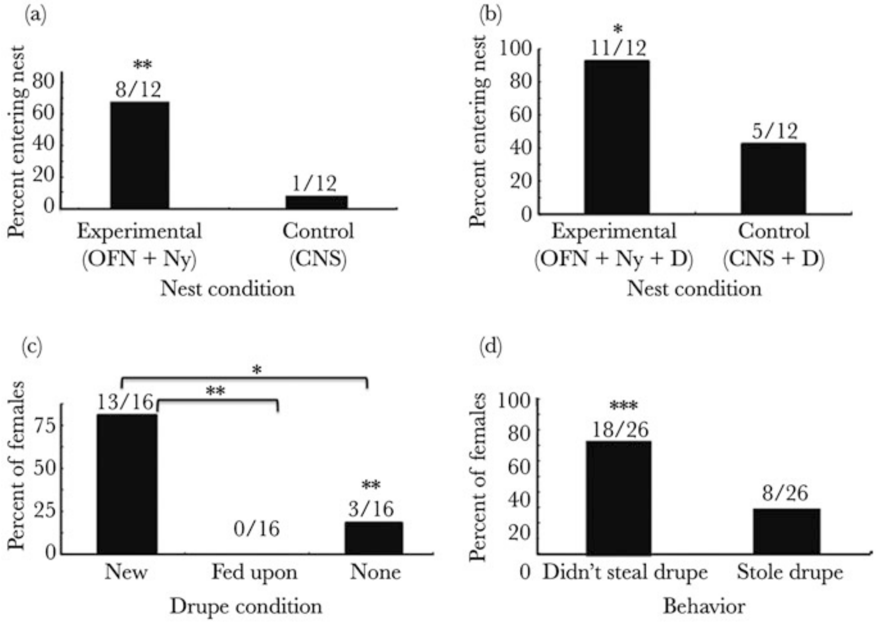


Fig. 6.32 Rate of intrusion into "other" female's nest and stealing behaviors of provisioning females. (**a** and **b**) *OFN* + *Ny* "other" female's nest with nymphs; *CNS* clean nest substrate (soil, leaf litter from field site); *D* drupe. *Fisher's Exact test, $p < 0.05$; **$p < 0.005$. (**c**) Females entered and then left intruded nest with a new drupe, a fed on drupe, or no drupe (none). *$\chi 2$ Goodness of Fit test, $P < 0.05$. **$p < 0.001$. (**d**) test female's nest was switched with OFN; provisioning female entered her nest (in the OFN location) and subsequently left the nest with or without a drupe. ***$\chi 2$ Goodness of Fit test, $p < 0.0001$. Test females in (**a**), (**b**), and (**c**) had not provisioned before the trial; test females in d had stolen one drupe prior to the trial. Adapted from Filippi and Nomakuchi (2016)

6.6.2 Testing the Attractiveness of a Good Drupe vs a Conspecific

To test whether the attractive force of a conspecific nest with a drupe was stronger than that of a drupe alone, the trial was repeated, but this time the experimental nest was either a conspecific nest containing a good drupe (>80% endosperm; $n = 12$) or a control nest containing clean substrate and a good drupe ($n = 12$), and the number of test females that entered each nest was counted. More than twice as many females entered the conspecific nest with the drupe compared to the control nest with the drupe (Fig. 6.32b; *, Fisher's Exact test, $p < 0.05$; Filippi and Nomakuchi 2016). Females were significantly more attracted to conspecific nests with a drupe than the control nests with a drupe, supporting the prediction that females are actively attracted to conspecific nests.

6.6.3 Could Females Be Entering a Conspecific Nest for Some Other Reason?

It is possible that females entered the nest to disturb the nest (interference competition) or that they mistook it for their own nest. To determine whether females were actually entering a conspecific nest to steal a drupe for the purpose of providing high-quality food for their nymphs, we placed one good drupe and one drupe that had been fed on extensively by nymphs in the experimental conspecific nest. We removed the lid on the test nest and monitored the female's behavior. For those that entered the experimental nest, we observed the female until it left the experimental nest to determine if a drupe was stolen, and if so, which one ($n = 16$). All 16 females entered the experimental nest. No females stole the fed-upon drupe and over four times as many females emerged with the good drupe, compared to those who emerged with no drupe (Fig. 6.32c; $*\chi2$ Goodness of Fit test, $P < 0.05$. $**p < 0.001$; Filippi and Nomakuchi 2016), supporting the prediction that females were entering conspecific nests to steal a good drupe.

6.6.4 Does the Female Find Her Own Nest and Other Nests by Location or by Odor?

To determine whether the sequence of behaviors by nest kleptoparasites happens via odor or location cues and whether females return to their own nest using odor or location cues, we allowed a female to leave her nest and steal a drupe from the experimental nest. After the test female returned to her nest with the stolen drupe and then set out to forage again, we quickly switched the location of the two nests and placed a fresh drupe in the putative conspecific nest ($n = 26$). We monitored the female to determine whether she would enter the putative experimental nest and whether she would leave with the drupe. All females entered the putative conspecific nest; however, less than half of the females emerged from the nest with a drupe (Fig. 6.32d; ***$\chi 2$ Goodness of Fit test, $p < 0.0001$; Filippi and Nomakuchi 2016), suggesting that females approached the previously visited experimental nest by location cues and then, recognizing that the nest was their own nest using chemical cues, did not remove a drupe.

6.6.5 Conclusions

The findings support the hypothesis that nest kleptoparasitism is not merely an opportunistic behavior but is an evolved tactic within the larger foraging strategy during progressive provisioning. Outside of the Hymenoptera, to the best of our knowledge, this is the first report of conspecific kleptoparasitism that involves approaching a victim's nest when it does not contain a resource reward. Females are actively attracted to the nests of conspecifics (Fig. 6.30a); they preferred to enter nests of conspecifics that contained a good drupe rather than clean substrate with a good drupe (Fig. 6.30b), entered nests to steal good drupes (Fig. 6.30c), and could distinguish their own nest using volatile cues even when it was switched with the conspecific nest and so did not remove drupes from it (Fig. 6.30d). Thus, in addition to progressive provisioning (Tsukamoto and Tojo 1992; Filippi-Tsukamoto et al. 1995), feeding limited to nymphs and inseminated females (Tsukamoto et al. 1994), suppression of metabolic rate to sustain the adult stage for up to 2 years in the absence of feeding (Tojo et al. 2005), selective foraging behavior (Nomakuchi et al. 1998), complex navigation behaviors during provisioning (Hironaka et al. 2003a, b, 2007a), production of trophic eggs (Hironaka et al. 2005; Filippi et al. 2012), and behaviors to defend against kleptoparasitism (Hironaka et al. 2008b), nest kleptoparasitism as an alternative tactic during provisioning is yet another evolutionary innovation that has enabled *P. japonensis* to optimize use of the severe resource constraints that it has experienced over its evolutionary history.

Considering that females have effective defense strategies against nest intruders (Hironaka et al. 2008a, b), it is curious that females preferred to enter conspecific nests with a drupe over clean substrate nests with a drupe. However, an earlier study demonstrated that females were absent from the nest at nearly 70% of the inspections, likely out foraging (Filippi et al. 2005); thus, there is a good chance that the intruding female will not meet with resistance. And should the resident female be present in the nest, it is also possible that she will be weakened from provisioning over many days and would not be a formidable defender. Thus, the cost of stealing might not be significant.

Another curious aspect of the host tree also suggests why attraction to a stockpile of drupes might be favored. The host tree grows in such a way that certain twigs produce and drop good drupes, while others do not, leaving hotspots of drupes on the ground. If a hotspot is encountered, the female will remember it and, using its keen navigation behaviors, return to it repeatedly. A well-provisioned nest would resemble a hotspot, and, with a bit of tweaking, co-opting the sensory and behavioral mechanisms used during provisioning to target conspecific nests would be a very efficient way to forage, indeed (Breed et al. 2012). Moreover, females clearly recognize the odor of other nests and avoid them when returning to their nest with a drupe because they never mistakenly provision conspecific nests (Filippi-Tsukamoto et al. 1995; Filippi et al. 2000; Hironaka et al. 2007a). To adopt the alternative tactic of nest thievery, they would then be attracted to the conspecific nest.

Other conditions that favor the evolution of nest thievery are the high density of nests with stockpiles of drupes in the foraging area and the fact that the stockpiles of drupes have already been vetted by females and so would require less handling time. Compared to self-foraging, the shorter amount of time spent exposed to predation and aggressive encounters with other provisioning females while foraging would be attractive (Broom and Ruxton 1998). These factors should also weigh heavily in favor of adopting the alternative tactic of nest kleptoparasitism. Females with the ability to be attracted to both drupes and conspecific nests should enjoy considerable success. If that ability is genetic, the trait and nest kleptoparasitism as an alternative foraging tactic should be favored by natural selection for provisioning females.

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Lisa Filippi initiated the work on *Parastrachia japonensis* at Mt. Hinokuma Park in Kanzaki Town, Japan, where she earned her M.S. and doctoral degrees elucidating many of the amazing physiological and behavioral traits of this fascinating insect through field and laboratory studies. She is currently a Professor of Biology at Hofstra University in New York.