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Alternative Methods of Nest Provisioning in the Digger Wasp *Clypeadon laticinctus* (Hymenoptera: Sphecidae)

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ABSTRACT: In a large nesting aggregation of the digger wasp *Clypeadon laticinctus*, all ($n = 18$) marked females under observation provisioned their nests with ants captured outside the nesting area. However, at least three other nests were provisioned by unmarked wasps who repeatedly took ants from neighboring nests.

Individuals varied in their ability to maintain possession of a nest and in the rate of bringing prey to the nest. Provisioning rate was proportional to body size. Although nests were not occupied by more than one wasp at a time, 25% of a sample of 29 nests changed ownership.

In sphecid wasps, hunting is done exclusively by adult females, who capture arthropod prey as a food supply for their offspring. The behavioral specializations involved in locating, capturing, and transporting prey have been analyzed in conjunction with morphological evidence to trace probable evolutionary pathways within the Sphecidae (Evans, 1963, 1966; Evans and West Eberhard, 1970). These studies involved comparisons among species or higher level taxa, with some attention to patterns of geographic variation within species. Gathering data adequate for making comparisons at such levels does not require that detailed attention be given to variation in the behavior of individual wasps. Consequently, few studies provide information on individual differences in rates of provisioning, nesting success, etc. Those relevant studies that exist show that individual variation occurs (Miller and Kurczewski, 1973; Alcock, 1975; Brockmann and Dawkins, 1979; Brockmann, 1980; Cowan, 1981). Variability, if heritable, is the raw material necessary for the evolution of the diversity we observe in hunting and provisioning behavior of solitary wasps. Hence, a more complete understanding of the range of individual variation in behavior exhibited by members of a population should contribute to our understanding of how they have evolved.

This paper compares rates of provisioning and patterns of nest occupancy among adult females of *Clypeadon laticinctus* (Cresson), and documents the existence of alternative methods of nest provisioning in one population of this species. *C. laticinctus* is an extreme prey specialist, capturing only worker ants of the species *Pogonomyrmex occidentalis* (Cresson) (Ainslee, 1909). Descriptions of nesting biology in *Clypeadon* are in Hicks (1927) and Evans (1962), and predator–prey interactions are described in Alexander (1985).

Methods

During the summer of 1982, a large aggregation of *C. laticinctus* nested in the floodplain of the Cache la Poudre River in Fort Collins, Larimer County, Colorado. Between August 23 and September 10, observations were made on two

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groups of 10 nests within the nest aggregation. One of the two groups was watched for 2 hours each day, either in the morning or the afternoon, with the scheduling randomized over 1-week blocks. Observations were dictated onto a tape recorder and transcribed each night.

The wasps seen provisioning a nest in this study were marked for individual recognition with dots of colored enamel paint on the thorax, and their head width was measured to the nearest 0.05 mm with a Mitutoyo dial caliper. The nest being provisioned was marked with a numbered nail driven into the soil near the nest entrance.

Results

HISTORIES OF NEST OCCUPANCY: Some nests were consistently provisioned by the same wasp, whereas others changed ownership during the course of the study. I never saw two wasps provision the same nest on the same day, but five of the 20 nests were provisioned by different wasps on different days. Twelve nests were provisioned by only one wasp, but only four of these were active throughout the study period. No wasp activity was observed during scheduled observation periods at three nests.

Some of the nests that became inactive after one or two days of observation, or were not active at all during the study period, may have been nests where provisioning had been completed. Excavations to determine the fates of nests were not done because they were located so close together that it was not possible to reliably distinguish cells from adjacent nests.

Repeated observations were made on 18 marked wasps, of which four provisioned more than one nest. Two moved into nests that had previously been used by other wasps, one apparently started a new nest of her own, and the fourth moved into an abandoned nest (or drove out the previous owner?), and later abandoned this nest and started a new one. Another wasp was active on 9 out of 14 observation days, but was only seen provisioning once, on the third day of the study. On subsequent days, she often entered the nests of other wasps, but she was never seen taking ants from these nests or bringing ants to any of the several nests that she temporarily occupied. Finally, each of the other 13 wasps was only seen provisioning a single nest. One of these wasps, who provisioned a nest from August 22 to 30, was driven away from her nest by another wasp. On September 2, she repeatedly tried to enter the nest and was driven out by a wasp inside. She was apparently injured and unable to fly. No wasp was seen at this nest after September 2.

INDIVIDUAL DIFFERENCES IN RATE OF PROVISIONING: Each wasp left the entrance to her nest open while provisioning, and sealed it from inside with a plug of soil when finished. Consequently, the closing of the nest entrance could be used to define the end of a bout of provisioning. Presumably a wasp was not always hunting for ants while she was away from the nest, since she also needed food for herself. However, once a wasp brought an ant back to the nest, she would continue bringing in prey at fairly regular intervals until she closed the nest from inside. Hence the time when a wasp first returned to the nest with prey was used as a starting point for timing the duration of a bout of provisioning.

Seven wasps who consistently provisioned a nest for a week or more varied considerably in the amount of time spent provisioning and the number of ants brought to the nest from one observation period to the next. The rate of provi-

Table 1. Nests robbed by "thief" wasps.

Nest being provisioned	Nest from which prey were taken
#53	#46 (2 prey) #61 (1 prey) #45 (1 prey) unknown (3 prey)
#57	#58 (16 prey) #54 (1 prey) #46 (3 prey) unknown (3 prey)
#55	#60 (1 prey)
Unknown nests	#61 (1 prey) #46 (2 prey)

sioning was positively correlated with wasp head width (Spearman's rho = 0.89, $P < 0.05$). The mean head width of these seven wasps was not significantly different from that of a sample of 35 other wasps caught during the study (Student's t-test, d.f. = 40, $t = 1.835$, $P > 0.05$).

NEST ROBBING: A few wasps obtained prey by stealing them from the nests of their neighbors rather than by hunting at ant mounds. This behavior was observed in unmarked wasps provisioning three different nests. One of these wasps was marked after she had stolen several ants, but she did no more provisioning that day and was not seen on subsequent days. The most extensive records on nest robbing are from a nest that was provisioned exclusively with stolen prey on 3 consecutive days. Two other nests were also provisioned in this way during one observation session. At least five different nests were robbed, and a wasp provisioning her nest by robbing would pilfer more than one nest (Table 1).

If the occupant of a nest was inside when a potential thief tried to enter, she usually drove the intruder away. Only twice (out of 34 occasions) was an ant taken from a nest while the occupant was inside. On one occasion, the thief dug into a nest about 30 minutes after the occupant had finished a provisioning bout and had sealed the nest entrance from inside. The thief took one ant and did not return. On the other occasion, the owner of the nest was in the middle of a provisioning bout, and the thief entered the nest while she was away. The owner returned with an ant while the thief was still inside, and 6 seconds later the thief emerged with an ant. Fifty-two seconds later, a small unmarked wasp entered the nest and was immediately driven away without prey. The owner of the nest continued provisioning, and one more ant was stolen from her nest while she was away.

With the one exception described above, all observed cases of nest robbing occurred when the wasp being robbed was provisioning her nest. At such times, the nests were left open, ants were available to be stolen (they were temporarily stored in the upper parts of the burrow while a wasp was provisioning), and the occupant of the nest was not present to defend her cache.

Discussion

Few insects invest as heavily in parental care as the aculeate Hymenoptera (Eickwort, 1981). Even in solitary bees and wasps in which the mother has no contact with her offspring after laying her eggs, she provides them with a complete

food supply and the shelter of a nest in which to grow and develop. The proposed adaptive significance of such extensive parental care is that it increases the survivorship of the offspring, although it also restricts the number of offspring an adult can produce (Eickwort, 1981).

Because constructing and provisioning a nest are so closely linked to female reproductive success in solitary wasps and bees, any heritable variability in these behaviors should have considerable adaptive consequences. This study documents the existence of variability in methods of provisioning, patterns of nest occupancy, and rates of provisioning in a population of *C. laticinctus*. A statistically significant positive correlation was found between a wasp's size and the rate at which she was able to provision a nest. The reasons for this correlation are unknown. It is possible that a larger wasp can subdue prey more easily. Furthermore, agonistic interactions between female *C. laticinctus* were often seen at hunting sites (Alexander, 1985). Large size may be advantageous in such encounters, as it is in agonistic interactions between male wasps (e.g., O'Neill, 1983; O'Neill and Evans, 1983).

However, it is not clear how much the reproductive success of individual wasps was affected by the observed differences in provisioning rates. The fact that some individuals were apparently driven away from their nests, or perhaps unable to provision a nest at all, suggests that the critical sources of variation in reproductive success may not reside solely in hunting efficiency. It may be equally important for a wasp to be able to defend a nest where her offspring can develop, and to insure that the prey she captures will feed her own offspring rather than those of a parasite.

Further studies of individual variability should increase our understanding of how alternative behaviors can be present within populations, and what the adaptive consequences of such variability can be. Of particular interest will be studies to elucidate the mechanisms that produce such variability, and the nature of the selection pressures maintaining behavioral polymorphisms within populations.

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