

Population Ecology

Food availability affects *Osmia pumila* (Hymenoptera: Megachilidae) foraging, reproduction, and brood parasitism

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Abstract Food limitation can reduce reproductive success directly, as well as indirectly, if foraging imposes a risk of predation or parasitism. The solitary bee *Osmia pumila* suffers brood parasitism by the cleptoparasitic wasp *Sapyga centrata*, which enters the host nest to oviposit while the female bee is away. I studied foraging and reproduction of *O. pumila* nesting within cages stocked with rich or sparse floral resources, and the presence or absence of *S. centrata* to test (1) the response of nesting female *O. pumila* to food shortages, (2) the response of nesting female *O. pumila* to the presence of parasites, and (3) whether brood produced under scarce resources are more likely to be parasitized by *S. centrata*. The rate of brood cell production was significantly lower in cages with sparse floral resources, although females in sparse cages did not produce significantly fewer brood cells overall. *Sapyga centrata* did not influence the rate of brood cell production, but females exposed to the cleptoparasites had marginally significantly lower reproductive output. Nests in parasite cages had significantly

fewer brood cells than those in parasite free cages. The mean duration of foraging bouts made by female *O. pumila* in sparse cages was not significantly longer than that in rich cages. *O. pumila* spent less time in the nest between pollen and nectar foraging bouts in sparse cages with *S. centrata* than those in other cages suggesting that these individuals made more frequent food foraging trips. Despite the weak effects of parasites and bloom density on foraging behavior, *O. pumila* brood cells experienced a 15-fold higher probability of parasitism by *S. centrata* in cages with sparse bloom than in those with rich bloom. These results support the hypothesis that indirect effects of food scarcity increase *O. pumila* susceptibility to brood parasitism, although the exact mechanism is not entirely clear yet.

Key words Apoidea · Cleptoparasite · Foraging · Induced defense · Trade-off

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Introduction

Food limitation can reduce reproductive success directly, as well as indirectly, if foraging imposes a risk of predation or parasitism (Abrams 1993). Organisms able to modulate their behavior to reduce these risks should improve their fitness, for example by maximizing the ratio of energy gain to mortality (Gilliam and Fraser 1987; Werner and Anholt 1993).

Empirical support for the general idea that foragers can balance conflicting demands of obtaining resources and avoiding predation comes from diverse systems including vertebrates and invertebrates (Sih 1980; Richards 1984; reviewed in Lima and Dill 1989; Bowers 1990; Gotceitas 1990). Organisms that cannot assess risk accurately, or that lack the flexibility to respond to the risk, may experience disproportionate costs from resource depletion.

Female solitary nest-making Hymenoptera must both obtain resources to provision offspring and protect the nest from a range of parasites and predators (Linsley 1958). Therefore, they may experience a trade-off between foraging and predation. The more time a bee allocates to foraging, the more offspring she can produce, at least until offspring production becomes limited by other factors, such as the rate of oocyte maturation (Rosenheim et al. 1996), or nest sites (Barthell et al. 1998). But the longer the female spends foraging, the greater the opportunity for certain types of brood parasites and parasitoids to enter the nest. A diverse array of brood parasites attack the nests and stored larval provisions of solitary bees

(Hymenoptera: Apoidea), spanning several insect and arachnid orders (Coleoptera, Diptera, Hymenoptera, Neuroptera, and Acarina) (Linsley 1958; Wcislo and Cane 1996). The two main categories of parasites: parasitoids, which consume the developing bee (e.g., Hobbs and Kronic 1971), and cleptoparasites, which kill the host egg and consume the pollen-and-nectar provision mass (Wcislo 1987; Michener 2000), differ in their strategies for obtaining access to the host nest. Host foraging behavior will most likely influence the success of those parasites that enter the nest and lay eggs directly in the brood cells, because the presence of the female in the nest often can deter these parasites (Eickwort et al. 1996). Nests of solitary Hymenoptera are particularly suitable for study of parasitism because they preserve a semi-permanent record of the fates of the offspring within, as well as the identity of brood parasites (Rosenheim 1987b).

Parasitic insects probably play a major role in the population regulation of bees (Szymas 1991 in Watmough 1983; Wcislo and Cane 1996), although few studies have reported their demographic effects. Selection pressure by parasites is thought to have favored the evolution of sociality in some groups of bees (Lin 1964; Lin and Michener 1972; Andersson 1984). In natural bee populations, parasitism rates vary widely among nests, populations, and species (Linsley 1958; Wcislo and Cane 1996). Variation in nesting behavior may influence parasitism rates. Michener (1985) posited that parasites searching for hosts in the two-dimensional habitat of ground-nesting bees would enjoy higher success rates than those searching in the three-dimensional habitat of stem-nesting bees, leading to greater parasitism rates in ground-nesters. A comparison of parasitism in 11 ground-nester/twig-nester pairs lent some support to the hypothesis (Wcislo 1996). Success of parasites also may depend on host density (Wcislo 1987). Theoretically, high host density could increase or decrease the likelihood of parasitism. Aggregations of hosts may concentrate parasites (Linsley 1958; Wcislo 1984) and may also be more apparent than isolated hosts (Rosenheim 1989). Conversely, high densities of conspecific hosts may improve protection by confusing parasites and predators. The hosts of parasites that search visually sustained higher rates of parasitism at low nest densities in one of two studies reviewed by Rosenheim (1990). Little conclusive evidence supports other hypotheses of inversely density-dependent parasitism, however (Rosenheim 1990).

The influence of resource competition on parasitism through behavioral trade-offs between foraging and nest defense has rarely entered discussions of variation in parasitism rates in solitary bees. Results from a field competition experiment between the introduced social bee *Apis mellifera* and the native North American solitary bee *O. pumila* indicated that under

competitive conditions, brood parasitism tended to increase (Goodell 2000). Because the primary parasite, the cleptoparasitic wasp *Sapyga centrata*, does not attack *Apis*, the effect of *Apis* is probably indirect: *O. pumila* nesting in sites with higher *Apis* densities alter their foraging behavior in ways that increase susceptibility of their nests to cleptoparasites. Under resource shortages, female *O. pumila* may make longer foraging bouts or more frequent foraging bouts to provision a given number of brood cells. The increased duration of bouts could reflect their foraging on flowers further from the nest, foraging on a greater number of flowers, or spending more time per flower. Any of these possibilities would increase the time spent out of the nest and potentially increase the opportunity for cleptoparasites to enter the nest unhindered.

Here, I present results of a controlled experiment examining the effect of floral resource availability on parasitism of *O. pumila* brood cells by the cleptoparasitic wasp *Sapyga centrata*. I used flight cages in which I could manipulate the availability of floral resources and the presence of brood parasites. I focused on three questions:

1. What are the effects of floral resource density on the rate of brood cell production and foraging trip duration?
2. What are the effects of the presence of parasites on brood production and foraging behavior?
3. Are brood cells provisioned under scarce floral conditions more likely to be parasitized than those provisioned under rich conditions?

If *O. pumila* alter their foraging behavior in the presence of brood parasites to improve protection of the nest (e.g., reduce the frequency or duration of foraging bouts), they should produce fewer brood cells. It would not be surprising if bees could not detect brood parasites, however, given the strong selection parasites must experience to evade detection. If bees increase their foraging effort under sparse resources, then parasitism of brood in sparse cages should be more likely than in rich cages. These outcomes do not imply mutually exclusive alternatives; females may both increase their foraging effort and still show reduced reproductive output if floral resource availability is low enough.

Materials and methods

Study system

Osmia (Melanosmia) pumila Cresson (Hymenoptera: Megachilidae) (Michener 2000) commonly inhabits oldfield and forest edge habitats in northeastern North America. Females of this univoltine solitary species make nests in preexisting holes in twigs or logs during May and June (in New York, USA). Working alone, they collect pollen and nectar to provision a linear series of brood cells within the cylindrical nests. Female brood cells are on average 20% longer than male brood cells (Goodell, unpublished data), and are constructed before the male cells so that female cells occupy the interior positions and male cells the exterior positions (Krombein 1967, K. Goodell, personal observation). *O. pumila* readily occupies “trapnests” made of wooden blocks drilled with deep holes (Krombein 1967; Goodell 2000). Nests made in trapnests can be stored at 4–5°C for 5–6 months and then warmed to promote emergence of the quiescent adults within.

Sapyga centrata Say (Hymenoptera: Sapygidae) attacks nests of *O. pumila*. Female *Sapyga* oviposit through the masticated-leaf partition of the most recently completed brood cell (Pate 1946; Torchio 1972). First-instar larvae of *Sapyga* kill and consume the host, then eat the pollen and nectar provision (Torchio 1972). *Sapyga centrata* develop into adults in late summer, then overwinter in the host nest, emerging with the surviving hosts in the spring. Torchio (1972) observed the related *Sapyga pumila* aggressively evicted by the host female when encountered in the nest, and often suffered damage to its antennae.

Experimental setup

I conducted the experiment in flight cages placed inside two greenhouse bays that were stocked with potted flowering plants. I used a complete factorial design with two bloom densities (rich and sparse) crossed with the presence and absence of the cleptoparasitic wasp *S. centrata*, for a total of eight cages and two replicates of each treatment combination. The wooden-framed cages (four within each bay) measured 2.1 m x 3.9 m x 2.1 m (width, length, and height, respectively) and were covered with fiberglass screening on the walls and a transparent plastic sheet on the roof. Each cage shared two sides with other cages. The long outer side of two cages per bay faced the outside window with eastern exposure (outer cages). The outer side of the other two cages faced toward the bay wall (inner cages); these had less

natural light than the outer two. I attached three 2.4-m-long banks of fluorescent lights to the ceiling of each cage (approximately 2 m from the floor) to provide a 15-h day length for the plants and to supplement the natural light while the bees were foraging. I used standard wiring of the lights. I maintained the temperature at 23°C from 0600 to 1700 hours and then cooled the bays to 14°C at night, although on hot sunny days the temperature rose in both bays up to 29°C. Because I expected the light environment to be the main source of unplanned variation among cages, I randomly assigned treatments to cages in the first bay and to opposing positions in the second bay, so that each treatment combination occurred in one inner and one outer cage.

Floral resources

I stocked each cage with blooming *Phacelia tanacetifolia*, *Trifolium repens* and *Fragaria* (a commercial variety). In addition, I provided each cage with one *Oenothera biennis*, the leaves of which *O. pumila* uses as nesting material. The *O. biennis* produced several flowers per plant, which *O. pumila* visited for nectar, but not pollen (personal observation). I provided four pots of blooming *Chrysanthemum* sp. in each of the cages that contained *S. centrata*. *Sapyga centrata* visits composites in the field, and visited the *Chrysanthemum* in the greenhouse. *Osmia pumila* did not visit *Chrysanthemum* in the greenhouse (personal observation).

I maintained the rich and sparse bloom densities by moving plants among the cages, checking every 3–5 days. I used the following units for quantifying bloom: plants for *Phacelia*, flower heads for *Trifolium*, and pots (containing five plants) for *Fragaria*. Each pot of *Phacelia* had 15–20 inflorescences with approximately five–ten open flowers that opened at a rate of two per inflorescence per day and lasted several days. An estimated 30–40 new flowers per *Phacelia* plant became available each day and 75–200 old flowers remained from previous days. After the initiation of the experiment, I learned that *O. pumila* used *Phacelia* as a primary pollen and nectar source, although they would also visit *Trifolium* for nectar, and only rarely would they visit *Fragaria*. Rich cages had twice as many *Phacelia* plants as sparse cages, although towards the end of the experiment when the bloom tapered off, I could not maintain that difference and still have *O. pumila* actively forage in all cages (Fig. 1). I provided proportionally more *Trifolium* in sparse cages to make sure the females in the sparse cages did not starve or stop nesting completely.



Fig. 1. Floral availability within flight cages of rich and sparse floral resources over the course of the experiment. The points show the mean number of pots (*Phacelia*: two plants/pot, and *Fragaria*: five plants/pot) or flowering heads (*Trifolium*) in each cage on days when plants were redistributed to maintain flower levels (see text). No error bars are provided because the counts were within one unit of each other in all cages within a resource treatment ($n=4$ cages). *Squares* = *Phacelia*, *triangles* = *Fragaria*, and *circles* = *Trifolium*. *Open symbols* are sparse and *filled symbols* are rich bloom densities

Bees and brood parasites

I collected all of the *O. pumila* and *S. centrata* wasps used in this study from nests in trapnests that I had placed in oldfield sites on Long Island, N.Y. during the spring of 1998 (Goodell 2000). I stored them at 5°C for 6 months starting in October and began warming bees at room temperature for emergence in late March. When an adult eclosed, I chilled it in the refrigerator, then marked its thorax with unique combinations of dots of Testors paint. I allowed male and female *O. pumila* to feed, mate, and acclimate to the experimental setup in a single cage. On 5 April, once I had 32 females and at least eight males, I randomly redistributed both bees and floral resources among the eight cages so that each cage had four female *O. pumila* and at least one male. I introduced additional males and females to the cages for another 5 days to ensure the opportunity for successful copulation; all cages ultimately received two–three males. Females that died within the first few days of the experiment were replaced as new females emerged. After 12 April, I ran out of replacement females, which left an unavoidably uneven distribution of three–five females per cage.

At the same time that I moved bees into their experimental cages, I placed trapnests in the northwest corner of each cage. These consisted of wooden blocks with 12 holes drilled in them of dimensions 12 cm long and 4 mm diameter. The holes were lined with translucent paper tubes (Custom Paper Tubes, Cleveland, Ohio).

As the *S. centrata* eclosed, I stored them in gelatin capsules at 12°C until I was ready to release them into the cages. On 20 April, the first day of host nesting, I released one female and two male *S. centrata* onto flowers in each of the four cages designated to receive parasites. I monitored the presence of *Sapyga* males and females daily and replaced those that disappeared.

Monitoring nesting and foraging

As female *Osmia* began nesting, I monitored the number of brood cells made each day by sliding the paper tubes from the nest holes and marking and dating the leading edge of cell construction on the outside of the paper tube. I did not replace completed nests with new straws immediately, but waited until the female had either begun a new nest or until there were only a few empty nest holes remaining in the block.

To measure foraging trip duration and frequency, I videotaped the nest entrances on 28 and 30 April, and 1, 2, and 5 May; all were fair-weather days during which the temperature inside the bays remained at 23°C. From 1000 to 1500 hours, I taped two–five blocks per day in a randomly chosen order; each block was taped on at least 2 days for 45 min. I narrated the tapes with my observations from within the cage on the activities of each nesting individual (pollen and nectar collecting, foraging for leaf material, or not foraging). I averaged the durations of foraging bouts and inter-trip intervals for each female across days. There was no significant trend in foraging bout durations over the five dates ($r=-0.19$, $n=36$, $P>0.1$, Fig. 2). Females can forage for food or for leaf material used in constructing partitions between brood cells. I did not distinguish between pollen foraging trips and nectar foraging trips (hereafter, “food trips”) because most females collected both in a single foraging bout. I did not expect the length of leaf foraging trips to vary with flower treatments.



Fig. 2. The mean duration of foraging bouts made by *O. pumila* females nesting in cages containing either sparse (*squares*) or rich (*circles*) floral resources, and *S. centrata* cleptoparasites (*filled symbols*) or no cleptoparasites (*open symbols*) over 5 days on which the bees were videotaped entering and exiting their nest holes. *Symbols* at the same point along the *abscissa* represent trips made by females within the same cage. *Arrows* indicate means comprised of leaf-collecting trips only

At the end of the experiment, I collected all of the nests and stored them in a loosely sealed box on a lab bench to allow the brood to complete their development. In September, I X-rayed the nests to examine the contents. I discovered then that many of the cells contained dead larvae and nearly complete pollen masses. This mortality potentially presented a problem: if both *O. pumila* and *S. centrata* eggs or larvae died, I would not be able to tell which cells had been parasitized. I dissected all of the nests and examined their contents under a dissecting scope, looking for the failed egg chorion or the *O. pumila* larva. I also looked for evidence

of parasitism, i.e., a second egg or larva. I found no evidence that *S. centrata* had failed in the egg or early larval stages of development. In a few cases, I found later larval instars that had died after the larva had begun defecating. These I could identify to species by the shape of the fecal pellets; most were *O. pumila*. From the X-rays, I measured the lengths of all of the brood cells except for those of four nests. Two bees nested outside of the nest block, one in a hollow bamboo plant stake and the other in a beetle burrow in the wooden frame of the cage. The lengths of these brood cells were not comparable to those of the rest of the sample because of the different nest diameters. Two nest tubes bent after repeated examinations, and the partitions had shifted from their original location before I could measure them.

Analysis

I performed analysis of variance using Proc GLM in SAS v. 8.2 for Windows (SAS 1999–2001) to test for effects of bloom density (bloom), the presence of *S. centrata* (parasites), and their interaction on four response variables: the rate of brood cell production; the total number of brood cells per nest; the mean brood cell length; and the number of brood cells per cage. All of the analyses were performed on cage means with a sample size of two. I tested for treatment effects on the mean brood cell length to make sure that response in the rate of brood cell production or total number of brood produced did not reflect a trade-off between cell size and number. Brood cell length is significantly positively correlated with the size of the pollen provision and adult mass of the bee within (Goodell, unpublished data). I treated brood cell size and the number of brood cells produced separately to avoid throwing out data on those nests for which I did not have length data. I have not found brood cell size/number trade-offs in natural populations of *O. pumila* (Goodell 2000).

I analyzed foraging trip and inter-trip durations for the effects of bloom, parasite and their interaction using analysis of variance as described above. There were not enough data to include trip type (food or leaf trip) in the model, so leaf trips were analyzed separately for effects of parasite treatment. Because all cages had the same density of leaf material for constructing partitions, I did not include bloom density as an independent factor. In all analyses, I interpreted P -values <0.05 as significant, and P -values of 0.05–0.08 as marginally significant.

I tested for effects of bloom density on the number of parasitized and unparasitized brood cells per cage with a logit model using Proc Catmod (SAS 1999–2001). This analysis is more powerful than an analysis of variance on the proportion of parasitized brood cells because

it takes into account the total number of opportunities for parasitism. This approach has the drawback that it assumes independence of brood cells within cages. I could not comfortably assume independence of cells within *O. pumila* nests in natural populations in the field because *S. centrata* probably maximizes the number of ovipositions by finding a few nests and then visiting them repeatedly for the opportunity to parasitize brood cells as they are made. This behavior has been suggested for several cleptoparasitic bees (Graenicher 1906; Michener 1953; Linsley and MacSwain 1955; Michener 1955; Rozen et al. 1978), and has been demonstrated for a chrysidid cleptoparasite (Rosenheim 1987a). In the cages, however, all nests were located in one nest block and search time for *S. centrata* should have been minimal. In fact, the *S. centrata* entered and checked repeatedly most of the holes within the blocks, suggesting successful oviposition depended less on finding nests than it would under natural conditions. Although I feel that the above analysis is the best approach given the limitations of these data, I interpret the results with caution because of the potentially higher type I error rate.

Results

The first bees began nesting on 20 April 1999; by 26 April, all cages had nesting bees. The peak of nesting lasted from 26 April to 8 May, after which the bloom began to decline and brood production ceased in the sparse cages. The three–five active bees per cage were distributed fairly evenly over parasite treatments, but the rich treatment had three more bees than the sparse treatment (Table 1). The main effect of this variation was to reduce the difference between the flower treatments because rich cages had on average more bees vying for the fixed amount of food (see Fig. 3 for flower unit:bee ratios). The test of flower availability, then, is conservative.

[Table 1. will appear here. See end of document.]



Fig. 3. Mean ratios of floral units:bees for four flight cages at the two bloom density levels. Means of floral units over sample dates in each cage were used to calculate ratios. Floral units are as described in Fig. 1. *Error bars* are 1 SD

Brood production

On average, female *O. pumila* nesting in rich cages produced 1.49 ± 0.13 SE ($n = 4$ cages) brood cells in a day, 48% higher than the 1.01 ± 0.04 SE brood cells produced by females in sparse cages (Fig. 4A). *Osmia pumila* in cages with *S. centrata* produced on average 1.14 ± 0.20 SE ($n=4$), or 17% fewer brood cells per day than the 1.36 ± 0.12 SE ($n=4$) brood per day produced by those nesting in cages without parasites (Fig. 4A). The analysis of variance revealed a significant effect of bloom density on daily brood production rates, but no significant effect of Parasites, nor a significant Bloom \times Parasite interaction (Table 2).



Fig. 4A–C. *Osmia pumila* nesting patterns across rich and sparse floral treatments, and the presence and absence of cleptoparasites. **A** Mean number of brood cells produced per day per female (mean of cage means). **B** Sum of the brood cells produced by *O. pumila* within each treatment combination (mean of cage means). **C** Mean number of brood cells produced per female per nest (mean of cage means). The error bars show 1 SE

[Table 2. will appear here. See end of document.]

The total number of brood produced per treatment reflects overall “reproduction potential” at the different bloom densities. In rich cages, *O. pumila* produced 60% more brood cells than in sparse cages (Fig. 4B), although this difference was not significant (Table 2). The 60% more brood cells produced under rich bloom was greater than the 23% more females, suggesting that the rich cages had not only higher absolute floral availability, but higher floral availability relative to the number of females than the sparse cages. Overall, bees nesting in bays with *S. centrata* made 29% fewer brood cells than those in cages without *S. centrata* (Fig. 4B), an amount not accounted for by the one extra (7%) female *O. pumila* in the parasite-free treatment. Interestingly, the parasite effect was slightly stronger than the bloom effect, although only marginally significant (Table 2).

The greater number of brood cells produced by *O. pumila* in the parasite-free cages reflects a greater number of brood cells per nest, rather than more nests. *O. pumila* nesting within cages containing parasites in either rich or sparse cages tended to distribute their brood over more nests relative to their counterparts in parasite-free cages (Fig. 4C). Nests in cages containing *S. centrata* had 5.88 ± 2.16 SE ($n=4$) cells, significantly fewer than the 9.11 ± 2.63 SE ($n=4$) per nest in cages without *S. centrata* (Table 2). Where *S. centrata* were present, rich

and sparse cages had similar mean numbers of brood cells per cage. Where *S. centrata* were absent, rich cages had on average 2.24 more brood cells per cage than nests in sparse cages, as reflected in the significant Bloom \times Parasite interaction (Fig. 4C, Table 2).

The mean length of brood cells per female show remarkably little variation, ranging from a mean of 6.39 ± 0.11 mm SE ($n=7$ females) in the rich/parasite cages, to 6.70 ± 0.32 mm SE ($n=6$ females) in the sparse/no parasite cages. There were no significant effects of bloom, parasite, or their interaction on mean brood cell length (Table 2), suggesting that size or sex ratio adjustments do not explain the trends in brood production across treatments.

Foraging behavior

I obtained foraging trip durations from video recordings of the nest entrances for two–five females per cage over 5 days. I recorded bees twice in every cage except for the second replicate of the sparse/parasite cage, which I only recorded once. In total, I obtained durations of 240 foraging trips and 254 inter-trip intervals from a total of 25 different female *O. pumila*. Because foraging bouts of female *O. pumila* did not vary significantly across the five recording dates, I used means across different sampling dates for the analyses. I omitted those trips and the subsequent inter-trip intervals that I could not identify as either a food trip or a leaf trip.

Food foraging bouts tended to last longer than leaf foraging bouts (food: mean = 227.5 ± 22.1 s SE, $n=22$ bees, leaf: mean = 83.37 ± 11.11 s SE, $n=11$ bees). I found no significant effects of bloom, parasite, or their interaction on the duration of food foraging bouts (Table 3), although they tended to be quicker in cages with parasites (Fig. 5A). Inter-trip intervals spent in the nest were longest in the rich/parasite treatments (Fig. 5B). The analysis of variance indicated a significant Bloom effect and a significant Bloom \times Parasite interaction (Table 3).

[Table 3. will appear here. See end of document.]



Fig. 5. The duration of **A** foraging bouts and **B** inter-trip intervals made by *O. pumila* females nesting in cages containing either rich or sparse floral resources, and *S. centrata* cleptoparasites or no cleptoparasites. *Error bars* show 1 SE

Leaf trip durations varied little among treatments, and there was no significant effect of parasitism. The intervals between leaf foraging bouts were also similar between parasite treatments (Table 3).

Brood parasitism

Sapyga centrata females spent their time foraging for nectar, investigating potential host nests at the nest block, and searching the cages for other nests. I recovered 14 parasitized brood cells of the 118 completed brood cells produced in this experiment for an overall parasitism rate of 12%. Four of these cells occurred in rich cages (mean = $5.0 \pm 0.01\%$, $n=2$), and ten in sparse cages ($25 \pm 0.20\%$, $n=2$). Brood cells in sparse cages had significantly higher parasitism rates (chi square=6.14, $df=1$, $P=0.013$). In fact, brood cells experienced a 5-fold higher probability of parasitism by *S. centrata* in cages with sparse bloom than in those with rich bloom.

Discussion

The results of this experiment provide unprecedented evidence that flower availability can influence not only nesting patterns and reproductive output in solitary bees, but the probability of brood parasitism. The small scale of the experiment, both in the number of bees, the number of cleptoparasites, and the number of replicate cages, however, suggest a cautious interpretation of these results until more data become available. Furthermore, the statistical analysis of brood parasitism required treating brood cells within cages as independent of nests and bees. While I feel that this approach is defensible in this particular situation, it is not a conservative approach, and therefore the parasitism results should be confirmed before confidently extending them to field situations. With those caveats in mind, I will go on to discuss the implications of these results. First, I will discuss the effects of food limitation, second, the responses of bees to cleptoparasites, and third, the interaction between food limitation and the presence of parasites.

Effect of resource availability

The daily rates of brood production of *O. pumila* in this experiment fell within the range of those of *O. pumila* nesting in trapnests in the field (0.50–2.5 cells/day, Goodell 2000). *O. pumila* nesting in sparse cages suffered reduced rates of brood production, although not

significantly fewer brood overall. Large variances within bloom density treatments may have resulted from a combination of my rather crude measures of resource availability or the unequal numbers of female *O. pumila* in the different cages. Nevertheless, the number of females nesting did not obviously influence the total number of brood cells made per female (Table 1). *Osmia pumila* did not respond to sparse resources by reducing cell size, a change which potentially could reflect a shift in sex ratios toward male production. Stability of *O. pumila* mean brood cell size under variable bloom densities contrasts with results of Kim (1999), who reported that *Megachile apicalis*, also a megachilid bee, produced a greater proportion of male offspring in cages with sparse flowers than rich flowers. Kim's cages were much smaller than those in my experiment, a design feature that might account for the difference in results. Theoretically, local resource competition among philopatric females might favor production of males if males disperse (Clark 1978). Highly male-biased sex-investment ratios in naturally occurring dense aggregations of the solitary bee *Calliopsis pugionis* support this hypothesis (Visscher and Danforth 1993). Lack of response in brood cell length may reflect ecological constraints imposed by reduced survivorship or reproductive success of small offspring (Tepedino and Torchio 1982, Stone et al. 1995, Kim 1997).

Floral availability had little effect on the duration of pollen and nectar foraging bouts. Inter-trip intervals were longer under rich resources, at least for *O. pumila* nesting in cages with *S. centrata*. One might expect longer inter-trip intervals in rich cages following food trips because larger pollen and nectar loads might take longer to deposit in the nest. Observations on the foraging behavior of a congener, *O. lignaria*, found that females returning to the nest with small amounts of pollen did not always deposit the pollen before returning to forage (N.M. Williams, personal communication), a behavior that would shorten the inter-trip intervals. I could not accurately gauge from the videos whether females had deposited the pollen while in the nest. If my estimates of foraging trip and inter-trip durations accurately measure foraging patterns throughout the day, they indicate that bees in rich cages made 18% fewer trips ($16.3 \text{ trips h}^{-1}$, maximum number of trips = 196 in 12 h) than bees in sparse cages ($19.8 \text{ trips h}^{-1}$, maximum number of trips = 238 in 12 h). A higher frequency of trips implies more time spent foraging.

Important differences between foraging in a small greenhouse cage and foraging in a natural setting may have limited the magnitude of response of *O. pumila* foraging trip durations to food availability. In a natural setting, bees can fly over a wider area in search of flowers if they became limiting, which could mean longer foraging bouts. In the field, *O.*

pumila pollen and nectar foraging bouts ranged from 120 to 1,200 s, while leaf trips remained relatively brief (K. Goodell, unpublished). We know little about the daily foraging radii of solitary bees. Anecdotal observations of the distance from the nest to known foraging sites estimate radii of 0.5–1.2 km (Kerfoot 1967; Eickwort and Ginsberg 1980; Visscher and Danforth 1993). Gathmann and Tschardt (2002) reported a positive relationship between body length and maximum foraging distance for 17 solitary bee species. This relationship predicts a 150-m foraging radius for bees similar in size to *O. pumila*, implying maximum foraging areas too large to replicate within the confines of enclosures. Natural populations also offer a more complex array of food sources than I could provide in the cages. In their natural environment, bees often can choose among more flower species that are distributed in a complex three-dimensional landscape, potentially increasing search time. For example, in natural populations of *O. pumila* on Long Island, N.Y. *O. pumila* used pollen from two–seven different plant species within a 5-day period (Goodell 2000). Bees probably use species based on their abundance, proximity, ease of harvest, or nutritional suitability, using less desirable species when preferred species are insufficient. Incorporation of less desirable species could increase foraging bout duration. Torchio and Bosch (1992) found that when the preferred pollen resource of *O. lignaria propinqua* occurred at low abundance, the bees visited at least ten additional flower species for pollen and nectar. Use of non-preferred floral resources has been noted even in some oligolectic bees if availability of the normal host is low enough (Linsley et al. 1963; Thorp 1969; Parker 1978). Although I provided several types of floral resources, microscopic analysis of the composition of many provisions revealed that the *O. pumila* rarely used *Trifolium* pollen, and apparently never actively collected *Fragaria* pollen (K. Goodell, unpublished). Rejection of *Trifolium* is puzzling because *O. pumila* visited it in the field, although infrequently as a pollen source. *Fragaria* pollen was not used by bees in the field, however (Goodell 2000).

Response to the risk of cleptoparasitism

Myriad aspects of the nesting biology of solitary Hymenoptera have been interpreted as adaptations to avoid parasites (Michener 1964; Evans 1966, 1977; Rosenheim 1989; Wcislo et al. 1993; Munster-Swendsen and Calabuig 2000). Most consideration of antiparasite behaviors has focused on fixed behaviors of species, such as the nest architecture, timing of nest excavation and provisioning, or tendency to aggregate. Few have reported plastic behaviors of hosts that can be induced by the presence of parasites. Solitary bees rarely attack

parasites that approach their nests (Wcislo and Cane 1996), although there are some reports of aggressive evictions of parasites found in the nest by a returning bee (Torchio 1972). Following the eviction of a parasite, females of some species knead the open provision mass with their mandibles, presumably to kill any parasite eggs left by the intruder (Torchio 1989, V. Scott, personal communication). This behavior may reduce parasitism by cleptoparasitic bees such as *Stelis* sp. that deposit their eggs underneath the host provision mass before the brood cell is closed (Rozen 1987), but would be ineffective against cleptoparasites that conceal their eggs within the brood cell wall or elsewhere within the host nest. Kneading also may be a common way for solitary bees to mix nectar and pollen to the right consistency for larval consumption (Torchio 1989), so may not have evolved specifically as an anti-parasitism strategy. Other behaviors, such as scratching on the inside of brood cell walls may target other types of cleptoparasite eggs (Rozen 1986).

My comparison of the foraging and nesting behavior of *O. pumila* in cages with and without cleptoparasites suggested that *O. pumila* respond to cleptoparasites not by making longer foraging bouts, but by spending more time in the nest between foraging bouts, although this pattern only held for bees foraging in rich cages. Another possible induced antiparasite behavior was the tendency for *O. pumila* to spread their brood over more nests in cages with parasites than those without. Rich cages showed a larger difference in mean brood cells per nest between parasite and no parasite treatments than sparse cages, perhaps because of greater numbers of brood cells overall. In the field, female *O. pumila* frequently abscond from a nest hole that has been disturbed excessively (personal observation). Such behavior in response to detecting parasites seems possible.

These modifications of foraging and nesting behavior could be cleptoparasite-induced responses to help defend against brood parasitism. The existence of induced defenses to cleptoparasites in solitary bees deserves more research attention. An experimental design that compares the foraging of bees just with and without parasites would allow more replication and increase the chances of detecting potentially subtle responses. A lack of evidence that bees can detect and respond to parasites would not be surprising. Parasites of bees have evolved elaborate mechanisms of concealing their activity from the host. Concealed placement of the parasite egg (see above), and chemical mimicry of the host by the adult parasite illustrate potential adaptations of parasites (reviewed by Wcislo and Cane 1996).

Indirect effects of resource stress

The probability of brood parasitism was higher in cages where food was less abundant, but the increased risk did not appear to reflect longer foraging bouts in sparse cages. Shorter breaks between foraging trips by bees nesting in sparse cages, however, may have meant both increased frequency of foraging bouts and less time allocated to protecting the nest. These modifications of foraging behavior may have provided more opportunity for the parasites in sparse cages to successfully enter and oviposit in the host nests.

Bees in both rich and sparse cages with parasites tended to spread brood cells over more nests than those in cages without parasites, although this effect was stronger in rich than poor cages. If fewer brood cells per nest (i.e., more nests) meant that *S. centrata* was less likely to encounter at least some of the brood cells, this response could help explain lower brood parasitism under rich resources. Because all nests were located in one nest block, however, this scenario seems unlikely. Reducing the number of brood cells per nest may be an antiparasite response that works under natural conditions, but not in the artificial setting of the flight cages.

The cleptoparasite *S. centrata* also may have benefited from the slightly slower rates of brood cell production if the slow rate implied that the sealed partition wall remained exposed longer in sparse cages than in rich cages. Bees that take longer to provision brood cells may increase their vulnerability to a wide range of cleptoparasites that oviposit directly onto the provision mass, as has been suggested, but not demonstrated (Torchio and Tepedino 1980; Danforth and Visscher 1993; Visscher and Danforth 1993). In the field, as bees spend more of their time foraging, they also may increase their exposure to parasites such as meloid beetles whose eggs or larvae on flowers can be picked up by bees and carried back to the nest. The probability that a bee will encounter one of these phoretic forms and carry it back to the nest presumably increases as some function of the number or diversity of flowers visited (Linsley and MacSwain 1952; Torchio and Bosch 1992). In addition, some evidence for the horizontal transmission of protozoan gut parasites among bees via covisitation to flowers (Durrer and Schmid-Hempel 1994) suggests yet another possible link between competitively induced changes in foraging behavior and the risk of parasitism in bees. Variation in food limitation may affect parasitism rates within and among host populations as much as factors such as aggregation of host nests. Differences among bee species or populations in parasitism

rates indirectly caused by resource competition may have contributed to the equivocal results of some comparative studies of parasitism rates (e.g., Rosenheim 1990; Wcislo 1996).

Clearly, the role of limiting floral resources in promoting parasitism needs more research. Enclosure studies offer a powerful way to begin testing the relationship between foraging and some types of parasitism, but field studies of natural populations must be used to examine how food-limitation influences foraging in a realistic setting. Comparative studies that examine how natural variation in foraging behaviors among individuals within a population relates to rates of brood parasitism could also contribute important information. These combined with experimental augmentations (or reductions) of floral resources could illuminate interactions between resource stress and risk of parasitism in solitary bees.

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Table 1. Summary of brood production data for each replicate cage within the experiment. Treatment combination is the bloom density/parasite level of the cage. Females is the number of *Osmia pumila* females that initiated at least one nest during the experiment. Nests is the total number of nests initiated in each cage. Brood cells is the sum of all brood cells within each cage. Fractions represent brood cells that a female had begun to provision, but not completed (all received a value of 0.5 cells). Parasitized cells is the sum of the brood cells containing *Sapyga centrata* cocoons or remains (see text)

Treatment combination	Replicate	Females	Nests	Brood cells	Brood cells/female	Parasitized cells
Rich/no <i>Sapyga</i>	1	4	5	55.5	13.9	
Rich/no <i>Sapyga</i>	2	5	6	58.5	11.7	
Rich/ <i>Sapyga</i>	1	3	4	24.5	8.2	1
Rich/ <i>Sapyga</i>	2	4	8	49.5	12.4	3
Sparse/no <i>Sapyga</i>	1	3	5	33.5	11.2	
Sparse/no <i>Sapyga</i>	2	3	6	47.5	15.8	
Sparse/ <i>Sapyga</i>	1	3	3	19.5	6.5	7
Sparse/ <i>Sapyga</i>	2	4	7	29.5	7.4	3

Table 2. Analysis of variance results for the effects of bloom density and *Sapyga centrata* presence (parasites) on the mean daily rate of brood cell production by *Osmia pumila*, the mean number of brood cells per nest, the mean brood cell length per nest and the total number of brood cells produced per cage. Significant results are in bold

	Brood cells per day			Mean cells per nest			Mean cell length per nest			Total brood cells per cage						
	df	MS	F	P	df	MS	F	P	df	MS	F	P				
Bloom	1	0.47	9.51	0.04	1	2.68	11.52	0.03	1	0.01	0.43	0.55	1	427.8	3.72	0.13
Parasite	1	0.09	1.88	0.24	1	17.8	76.57	0.001	1	0.12	3.92	0.12	1	657.0	5.71	0.08
Bloom × parasite	1	0.02	0.35	0.59	1	2.9	12.47	0.02	1	0.07	2.30	0.20	1	7.0	0.06	0.82
Error	4	0.49			4	0.23			4	0.03			4	115.0		

Table 3. Analysis of variance results for the effects of bloom density and the presence of *Sapyga centrata* (parasite) on the duration of pollen/nectar and leaf material foraging bouts and inter-trip intervals (spent in the nest) by *Osmia pumila* females nesting in experimental cages. Significant results are in bold

Source	Food Trips				Leaf Trips			
	df	MS	F	P	df	MS	F	P
Duration of foraging trip								
Bloom	1	470.43	0.06	0.82				
Parasite	1	19,068.89	2.5	0.19	1	127.98	0.21	0.67
Bloom × Parasite	1	9,506.00	1.25	0.33				
Error	4	7,614.89			5	617.90		
Duration of inter-trip interval								
Bloom	1	1,114.6	25.12	<0.01				
Parasite	1	529.77	11.94	0.26	1	93.50	0.03	0.86
Bloom × Parasite	1	1,564.61	35.26	<0.01				
Error	4	44.37			5	2,807.80		