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A solitary ground-nesting wasp truncates its parental investment in response to detection of parasites

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Abstract. 1. Parental investment by solitary nest-building wasps and bees is predicted to be plastic, responding to variation in the sex of the offspring, the availability of food used as provisions (‘resource limitation’), the female’s inventory of mature oocytes (‘egg limitation’), and risk imposed by nest parasites.

2. I observed nest provisioning by *Ammophila dysmica*, a solitary, ground-nesting wasp that provisions its nest with one or two caterpillar prey to evaluate the hypotheses that provisioning is shaped by caterpillar size, offspring sex, the hunting time required to capture prey, a female’s egg load, and penetration of nests by the parasites *Argochrysis armilla* and *Hilarella hilarella*.

3. *Ammophila dysmica* were more likely to add a second provision to the nest when the first prey item was relatively small and when provisioning daughters.

4. Neither the hunting time required to capture the first caterpillar prey nor the female’s inventory of oocytes predicted a female’s likelihood of adding a second caterpillar to a nest. Variation in oocyte inventory across females was minimal; all females examined had a mature or nearly mature oocyte remaining in the ovaries immediately after laying an egg.

5. *Ammophila dysmica* were much less likely to add a second caterpillar to nests that were penetrated by parasites during the first provisioning.

6. Although many nest parasites have evolved adaptations to avoid detection by their hosts, oviposition by *A. armilla* often appears to reveal its presence, eliciting an abrupt truncation of investment by the host in that nest.

Key words. Brood parasite, egg limitation, nest provisioning, parasite detection, parental investment, resource limitation.

Introduction

Parental investment in solitary ground-nesting wasps and bees is predicted to be highly plastic. There is broad empirical support for two sources of variable nest provisioning behaviour. First, wasps that provision their nests with captured prey, which are discrete packages of food, frequently adjust the number of prey provisioned in response to the size of each prey to achieve the desired total amount of food provisioned (O’Neill, 2001). Second, many ground-nesting wasps and bees are sexually dimorphic, usually with females larger than males, and many studies have demonstrated that mothers must invest more to produce offspring of the larger sex (Helms, 1994; O’Neill, 2001; Danforth *et al.*, 2019). A recent phylogenetic analysis has demonstrated that a highly flexible nest provisioning strategy, based on adding a variable number of prey to a single nest, is ancestral in the family Sphecidae, a member of which I study here (Field *et al.*, 2020).

Two other potentially important sources of variable parental investment have received less empirical evaluation. First, parental investment is predicted to respond to changes in the likelihood that lifetime reproductive success of the mother wasp or bee will be constrained by the availability of resources used to provision offspring, or ‘resource limitation’, versus the availability of mature oocytes, or ‘egg limitation’ (Rosenheim *et al.*, 1996). Many solitary nest-building wasps and bees produce large oocytes (Iwata, 1964; Rozen Jr., 2003), and the time needed to mature these oocytes has been suggested to limit reproductive output for some wasps (Field *et al.*, 2007) and especially for bees (Danforth, 1989; Minckley *et al.*, 1994; Neff, 2008; Danforth *et al.*, 2019). Although

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studies manipulating the abundance or proximity of floral resources for solitary bees have demonstrated flexible parental investment (Kim, 1999; Peterson & Roitberg, 2006a, b), I know of no studies addressing the possibility that the availability of mature oocytes shapes nest provisioning. Theory predicts that egg-limited females should act to increase reproductive returns per egg laid by provisioning each offspring more generously; furthermore, the importance of egg limitation is predicted to increase when resources used to provision nests are especially abundant in the environment, such that the rate of nest provisioning exceeds the rate of oocyte maturation (Rosenheim *et al.*, 1996; Rosenheim, 2011; Segoli & Wajnberg, 2020).

Second, solitary wasps and bees often interact with a diverse community of parasites (Clausen, 1940; O'Neill, 2001; Danforth *et al.*, 2019; Minckley & Danforth, 2019), and theory suggests that optimal parental investment should respond to the global risk of nest parasitism, with greater risk favouring smaller investment in each offspring (Seidelmann, 2006). Although not yet explored with formal theory, it also seems likely that a mother wasp or bee that detects that a parasite has penetrated a cell or nest, signalling an elevated risk of parasitism, should also limit further investment in the invaded nest, and instead should initiate a new cell or nest where the expectation of successful reproduction will be higher. Goodell (2003) manipulated the presence/absence of the brood parasite *Sapyga centrata* in greenhouse cages with the bee *Osmia pumila* nesting in artificial trap nests, demonstrating that the host bees increased their time in the nest in the presence of parasites but did not alter the amount of food provided to each offspring. Field and Brace (2004) demonstrated experimentally that whereas the wasp *Ammophila pubescens* is unable to recognise the presence of newly deposited larvae of the brood parasitic fly *Metopia*, once the parasite is present for a day, which is long enough for it to kill the host egg, the mother recognises the failure of her nest, which she abandons. Brood parasites are known to exhibit a variety of stealthy behaviours, for instance producing dwarf eggs that they conceal by embedding them in the walls of the host cells (Danforth & Visscher, 1993; Rozen Jr., 2003) or by hiding their eggs under or within the mass of provisioned prey or pollen and nectar (Vinson *et al.*, 2011). Furthermore, parasites may exhibit chemical mimicry of their host (Strohm *et al.*, 2008; Wurdack *et al.*, 2015) or use materials in their host's nest as chemical camouflage (e.g., Torchio, 1989) to avoid leaving distinctive chemical traces of their visit. Thus, brood parasites appear to be under strong selection to reduce their detectability by their hosts (Rozen Jr., 2003; Litman, 2019), and simultaneously hosts appear to be under strong selection to improve their ability to detect parasites. To my knowledge, no studies have examined the possibility that wasps or bees might modulate parental investment in response to detecting cues associated with the presence of parasites in a particular cell or nest, short of outright abandonment of nests harbouring parasite-killed offspring (Field & Brace, 2004).

In some cases, wasps and bees appear to make decisions about the intended amount of provisions and offspring sex at the earliest possible point in the nesting cycle, when they construct the cell, building cells in two size classes, smaller cells to receive less provisions and produce the smaller offspring sex (usually sons) and larger cells to receive more provisions and produce the larger offspring sex (usually daughters; e.g., Brockmann & Grafen, 1989; Rooijakkers & Sommeijer, 2009). In this case, one might imagine that provisioning decisions could be less flexible at later stages of provisioning of each cell. If, however, there is just one class of cell sizes, provisioning decisions could respond conditionally to events occurring later, during the initial stages of nest provisioning. The ability to adopt a conditional provisioning strategy would seem to be especially important when unpredictable events, such as the size of a large, captured prey, or the attack of a parasite, change the most favourable strategies.

Here I report 6 years of field observations made on the solitary, ground-nesting wasp *Ammophila dysmica* Menke (Hymenoptera: Sphecidae). *Ammophila dysmica* excavate shallow unicellular nests and provision them with one, two, or very rarely three caterpillars (Rosenheim, 1987a). *Ammophila dysmica*, like other *Ammophila* spp., is sexually dimorphic, with females 1.57 times as heavy (dry weight) as males (Field *et al.*, 2015). I ask first whether there are two size classes of nest cells, with a smaller class destined to receive a single caterpillar provision and a larger class destined to receive two (or more) caterpillar provisions. I find no support for the presence of two classes of cell sizes, leaving open the possibility that *A. dysmica* adjusts nest provisioning in response to events occurring later, during the placement of the initial caterpillar provision into the nest and the laying of the egg. I address the following questions: (1) Do *A. dysmica* females adjust the number of caterpillars provisioned in response to the size of the first caterpillar captured? (2) Are *A. dysmica* females more likely to allocate multiple caterpillars as provisions for daughters versus sons? (3) Do *A. dysmica* females adjust nest provisioning in response to the time required to successfully hunt for a caterpillar or their inventory of mature oocytes? And (4), do *A. dysmica* reduce their likelihood of adding a second caterpillar to a nest that has been penetrated by a parasite during placement of the first caterpillar provision?

Materials and methods

Study system

Nest provisioning behaviour of *A. dysmica* was studied at the University of California Sagehen Creek Field Station in California's Sierra Nevada. Wasps nested in a series of loose aggregations alongside a dirt road located in the Sagehen Hills, elevation 2000 m (39.4233, −120.2361; for details on the study site, see Rosenheim, 1987a). *Ammophila dysmica* excavate shallow, unicellular nests, place a temporary closure on the nests, and then hunt for caterpillars on *Ceanothus velutinus* Douglas ex Hook and *Ceanothus prostratus* Benth. (Rhamnaceae) shrubs that dominate the understory. *Ammophila dysmica* sting captured caterpillars, inducing permanent paralysis but not killing them. Females place the first caterpillar into the nest and lay a single large egg on it; in 1988, mean egg length was 3.13 ± 0.61 mm (mean ± SE, $N = 29$). Immediately after oviposition, females either complete the nest, placing a permanent closure, or resume hunting for a second caterpillar provision for the nest, in which case another temporary closure is constructed to protect the nest during the hunting period. Both temporary and permanent closures include a tunnel-plugging pebble, a layer of dirt and pebbles that are firmly packed into place, and finally a loose jumble of pebbles and dirt; the firm-packed layer is largely impervious to parasites that may try to dig into the nest. Temporary and permanent closures are readily distinguishable, because only for the permanent closure do host wasps incorporate a distinct layer of organic material, made up mostly of dead arthropods collected on the soil surface in the nesting area, that is placed above the firm-packed layer (Rosenheim, 1987a).

Ammophila dysmica nests are attacked by parasites, of which the most important is *Argochrysis armilla* Bohart (Hymenoptera: Chrysididae), with a few nests also parasitised by *Hilarella hilarella* Zedterstedt (Diptera: Sarcophagidae) (Rosenheim, 1987a). *Argochrysis armilla* locate host nests primarily during the lengthy and conspicuous nest digging, learn the location of nests relative to local landmarks, and monitor a series of host nests for hours to days to await the return of the host with a caterpillar (Rosenheim, 1987b). *Argochrysis armilla* then attempt to penetrate the nest and lay a small clutch of eggs, which are firmly glued to either the caterpillar or the walls or ceiling of the cell (Rosenheim, 1987a, 1993). Although *A. armilla* will occasionally attempt to lay eggs in nests at times other than nest provisionings (e.g., at the end of nest digging, or by digging through temporary closures while the host is away hunting), these appear only very infrequently to be successful. Thus, nests that are successfully parasitised are almost always penetrated when the host has removed the nest closure and is placing the caterpillar provisions in the cell, and the host wasp is nearly always present in the cell during at least part of the time that *A. armilla* is laying its eggs (rare exceptions occur when, for example, the parasite completes its oviposition when the host wasp is searching for a pebble with which to plug the nest). *Argochrysis armilla* larvae feed indiscriminately on the caterpillar provisions and the host larva, nearly always resulting in the death of the host. *Hilarella hilarella* also generally attack nests during provisioning, but larviposit from aboveground, at the lip of the nest, dropping the larvae into the nearly vertical shaft of the nest (Rosenheim, 1987a; Spofford & Kurczewski, 1990). *Hilarella hilarella* larvae immediately seek out the host egg and kill it, and then consume the caterpillar provisions. Like *A. armilla*, multiple *H. hilarella* offspring often develop in each cell.

Observations were made during the summers of 1983 (10 July – 9 August, $n = 22$ nests), 1984 (30 June – 24 July, $n = 68$ nests), 1985 (30 June – 3 July, $n = 4$ nests), 1986 (22 June – 22 July, $n = 152$ nests), 1988 (22 June – 17 July, $n = 35$ nests), and 1991 (24 June – 1 August, $n = 78$ nests). Because data collection to study the influences on nest provisioning required destructive sampling of nests or nesting females, I emphasised different data collection goals during different years.

Two size classes of brood cells?

To test if there are two size classes of nest cells, destined to receive one versus two caterpillars, all nests observed were excavated to measure the dimensions of the brood cell (length, width, height) to the nearest 0.5 mm using a small ruler, either at the end of the nesting season (1983, 1984, 1985, 1986), immediately after the first caterpillar provision was added (1988), or after the final closure was placed on the nest (1991). Only dimensions not disrupted during the excavation process were recorded.

Consistent inter-individual variation in provisioning?

Although this study's goal was to examine factors that might shape conditional nest provisioning behaviour by individual *A. dysmica*, another possibility is that nest provisioning behaviour that is variable when viewed at the population level might reflect a mixture of females each of which is fixed in its expression of one of two strategies: either to always provision nests with a single caterpillar, or to always provision nests with >1 caterpillar. To assess this possibility, some females during the 1983 ($n = 11$) and 1984 ($n = 4$) field seasons were individually marked by applying different combinations of paint spots (Testors brand enamel) to the dorsum of the mesosoma, and then followed to record their nest provisioning behaviour across a series of sequentially completed nests.

Influence of caterpillar size

To test if *A. dysmica* adjust the number of caterpillars provisioned in response to the size of the first caterpillar captured, nests were excavated immediately after the first caterpillar provision was placed (1988) or after the final closure was placed on the nest (i.e., after either the first, second, or third caterpillar was provisioned; 1991), providing an opportunity to quantify caterpillar size before the caterpillars were consumed by the host wasp or parasites. In 1988, I observed initial nest provisionings and recorded whether the closure was temporary (i.e., no organic layer) or permanent. Nests were excavated later during the day of the first provisioning, and caterpillars were returned to the laboratory where they were preserved by being placed in boiling water for 3 min (to kill bacteria) and then transferred to 70% ethanol. Weights of ethanol-preserved caterpillars, blotted dry with paper towelling, were subsequently weighed on an ultramicrobalance.

During the 1991 field season, fresh weights of all caterpillars placed in fully-provisioned nests were measured by excavating the nests on the day of the final closure, retrieving the caterpillars, and weighing them on an ultramicrobalance.

Influence of offspring sex

To test if *A. dysmica* are more likely to allocate multiple caterpillars as provisions for daughters versus sons, nests observed during 1983, 1984, 1985, and 1986 were excavated at the end of the nesting season, when the offspring had completed their larval development and spun cocoons in which they would overwinter as prepupae. To determine the sex of *A. dysmica* offspring, overwintering prepupae in cocoons were returned to the laboratory, chilled at 4°C for ca. 4 months to simulate overwintering, and then placed in a shaded greenhouse at ca. 27°C to break diapause and trigger emergence. Only for *A. dysmica* offspring collected in 1986 did this protocol fail to break offspring diapause; for these offspring, during the late fall of 1987 the unemerged cocoons were placed in plastic tubes fitted with fine metal mesh windows, returned to the study site, buried at ca. 50 mm depth (the natural depth of an *A. dysmica* cells), and overwintered a second year to obtain successful emergence in the summer of 1988. I was generally unable to rear *A. dysmica* larvae in the laboratory once nests had been excavated, thus no information on offspring sex were available for 1988 and 1991.

Influences of hunting time and egg load

To test if *A. dysmica* adjust nest provisioning in response to the relative risks of time limitation versus egg limitation, I measured the time required to successfully hunt for a caterpillar and the females' inventories of mature oocytes. During each year of the study, I measured the hunting time required to capture the first caterpillar provision for each nest. This was quantified as the time between the completion of nest digging and the female's return to the nest with the first caterpillar. All intervening time between 09:00 and 18:30 h was assumed to be spent in active hunt; observations of wasps supported this interpretation, although wasps were observed to interrupt their hunting periodically for short bouts of feeding on floral nectar (Rosenheim, 1987a). Nest provisioning was very rapid, and thus many provisionings were not observed; consequently, sample sizes were much smaller than the total number of nests recorded each year.

During the 1988 field season, I gathered egg load data to evaluate the hypothesis that *A. dysmica* oocyte inventory at the time of the first nest provisioning influenced the decision to add a second caterpillar. I observed first nest provisionings and recorded whether the closure was temporary (i.e., the female intended to add another caterpillar) or permanent. Females were then collected, immediately put into Bouin's solution fixative, and returned to the laboratory for dissection of the ovaries under a stereomicroscope. Using an ocular micrometer, I measured the length of the largest oocyte in each of the six ovarioles. In *A. dysmica*, larger females lay larger eggs (linear regression of head width on egg length, coefficient for head width = 0.406 ± 0.113 (SE), $N = 29$, $r = 0.57$, $P = 0.0012$). Therefore, following O'Neill *et al.* (2015), to standardise oocyte measurements for variation in female size, oocyte lengths were divided by the female's head width. Two indices of egg load were then calculated: (i) the standardised length of the single largest oocyte, and (ii) the sum of the standardised lengths of the largest oocyte in each of the six ovarioles (O'Neill, 1985).

Influence of parasites

During all field seasons, first and second nest provisionings were observed to record immediate threats posed by parasites to determine if such threats shape *A. dysmica* nest provisioning decisions. For *A. armilla*, I recorded whether parasites successfully penetrated the nest, staying below ground for at least 10 seconds (i.e., time sufficient for oviposition) at any time between the removal of the temporary closure and the replacement of the plug pebble in the nest burrow. For *H. hilarella*, I recorded actual larviposition, which could be observed directly, since these parasites drop larvae into the tunnel of the nest from the lip of the nest entrance, aboveground.

Nest provisioning and nest outcomes

For the 1983, 1984, 1985, and 1986 field seasons, the number of caterpillars placed in each nest was determined either (i) through direct observations of the provisionings, when these were witnessed, or (ii) by excavating nests after development of the *A. dysmica* offspring or nest parasites was complete, and recovering the caterpillar head capsules. Head capsules were the only body parts of the caterpillars that were never consumed by cell occupants. Nest outcomes for these field seasons were determined by whether the nest yielded an *A. dysmica* cocoon (unparasitised) versus *A. armilla* cocoons or *H. hilarella* puparia (parasitised); nests containing only dead, moldy contents were excluded. For the 1988 and 1991 field seasons, I excavated nests before occupants had completed their development. In 1988, I recorded the intention of the host female to provision the nest with a single caterpillar versus >1 caterpillar based on the type of closure placed on the nest after the first caterpillar was provisioned (temporary versus permanent). Nest outcomes were determined for nests that received a final closure by whether only the host larva was found (= unparasitised) or whether the brood cell contained eggs of *A. armilla* or larvae of *H. hilarella* (= parasitised). For the 1991 field season, all nests were excavated on the day they received their final closure, and caterpillars were counted and weighed. The first caterpillar was always recognizable as the one that bore the *A. dysmica* egg. Nest outcomes were recorded as for 1988, based on immature stages of the host and parasites recovered.

Statistical analysis

The ideal analysis would have been a single statistical model examining the joint influences of all of the predictors of interest (caterpillar size, offspring sex, hunting time, egg load, and parasite presence) on nest provisioning decisions by *A. dysmica*. But measuring some of the predictors precluded the measurement of other predictors (for instance, measuring caterpillar weights made it impossible to rearing offspring and determine their sex). Furthermore, had I attempted to include all predictors in a single model I would have had few complete cases, because many predictors were measured only intermittently (e.g., it was difficult to record parasite penetration into nests during the first provisioning, because provisioning was rapid and I needed to detect the female's presence at the nest within seconds of her arrival to obtain a definitive record). Thus, a more pragmatic approach was to build a series of statistical models to test the roles of different subsets of predictors.

To test the hypothesis that *A. dysmica* females produced two classes of cells, smaller cells destined to receive a single caterpillar and larger cells destined to receive two (or more) caterpillars, I used two-way ANOVA, with main effects for year and the number of caterpillars subsequently added (1 versus >1) as predictors of cell dimensions (length, width, and height). (The number of nests for which cell dimensions were measured and offspring were successfully reared was too small to test for offspring sex-specific cell dimensions.) Generalised linear models with a binomial error distribution and a logit link function were used to evaluate influences of continuous predictor variables (first caterpillar weight, maternal egg load, maternal head width, hunting time) on nest provisioning behaviour (nests provisioned with 1 versus >1 caterpillar). To include any possible influences of changing conditions within a nesting season (i.e., effects of maternal age, or seasonal changes in the environmental conditions, including possibly caterpillar size), the day of the nesting season was included as a fixed effect, as was year for analyses that included data from more than 1 year. To evaluate the influence of categorical predictor variables (offspring sex, parasite penetration of nests during the first provisioning) on provisioning behaviour, I conducted Asymptotic Generalised Cochran–Mantel–Haenszel tests, with stratification by year; these are permutation tests, implemented in R package '*coin*' (Hothorn *et al.*, 2019), and have the advantage of being free of assumptions about the underlying distributions of the response variables. All tests were two-tailed. All analyses were performed in R version 3.5.2 (R Core Team, 2018). Unless stated otherwise, means are reported ±1 SD.

Results

Do females decide on the number of provisions at nest construction?

I found no support for the hypothesis that *A. dysmica* decide to produce a nest that will receive one versus >1 caterpillar provision during nest excavation. The dimensions of brood cells that subsequently received a single caterpillar did not differ from the dimensions of brood cells that received a second caterpillar (2-way ANOVA, with main effects for the number of provisions and year, effects on cell length, width, and height all NS, $P > 0.25$). Cell lengths were 18.1 ± 2.27 mm ($n = 84$) and 18.3 ± 2.53 mm ($n = 33$) for nests receiving one versus >1 caterpillar, respectively; corresponding cell widths were 10.6 ± 1.3 mm ($n = 80$) and 10.9 ± 1.4 mm ($n = 36$), and cell heights were 10.1 ± 1.2 mm ($n = 19$) and 10.2 ± 1.5 mm ($n = 12$); sample sizes varied because many cells were too damaged during excavation to obtain measurements. Thus, *A. dysmica* do not appear to adopt a provisioning strategy at the time of nest construction, preserving flexibility to respond to later events.

Consistent inter-individual variation in provisioning?

Only five of the females that were individually marked during 1983 and 1984 were seen to provision ≥3 cells over their reproductive lifetimes for which I recorded the provisioning strategy. These admittedly fragmentary data are not consistent with the hypothesis that females adopt fixed provisioning strategies across nests: 3 of the 5 females provisioned one caterpillar in some nests and two caterpillars in others (sequences: 2–1–2-1; 1–1–1-1-2; 1–1–1-2-2). The two remaining females produced only singly-provisioned nests (sequences: 1–1–1-1-1; 1–1-1).

Caterpillar size

In both years for which I gathered data on caterpillar weights, 1988 (Fig. 1) and 1991 (Fig. 2), *A. dysmica* were more likely to add a second caterpillar to a nest when the first caterpillar provisioned was relatively small (GLM: 1988, coefficient for caterpillar weight: −96.6 ± 38.6 (SE), $P = 0.012$, Appendix S1; 1991, coefficient for caterpillar weight: −29.6 ± 8.2 (SE), $P = 0.0003$, Appendix S2). When first caterpillars weighed less than 0.15 g, *A. dysmica* almost always supplemented the nest with a second caterpillar, whereas when first caterpillars weighed more than 0.20 g, *A. dysmica* almost always completed nest provisioning with just that single caterpillar. When *A. dysmica* did hunt for a second caterpillar, the caterpillars captured were slightly smaller on average (0.140 ± 0.0117 (SE) g, $n = 24$) than the caterpillars used for the first provisions (0.164 ± 0.0071 (SE) g, $n = 58$), but the difference was marginally non-significant (ANOVA, $F_{1,80} = 3.21$, $P = 0.077$). Nevertheless, nests that received >1 caterpillar received a greater total mass of provisions (0.288 ± 0.0151 (SE) g, $n = 22$) than did nests that received only a single caterpillar (0.191 ± 0.0088 (SE) g, $n = 31$; ANOVA, $F_{1,51} = 35.3$, $P < 0.0001$; Fig. 2).

Offspring sex

As hypothesised given that *A. dysmica* is sexually dimorphic with larger females, there was a significant association between the sex of the offspring and the number of caterpillars provisioned (Fig. 3; asymptotic Generalised Cochran–Mantel–Haenszel test, stratified by year, $\chi^2 = 6.90$, df = 1, $P = 0.0086$); most 1-caterpillar nests produced sons, whereas most 2-caterpillar nests produced daughters.

Limitations imposed by availability of caterpillars and mature oocytes

I found no support for the hypothesis that nest provisioning is influenced by changing constraints imposed by the difficulty of securing provisions or by the mother's finite inventory of maturing oocytes (egg load). A Generalised Linear Model of provisioning data across all years for which data on hunting time for the nest's first caterpillar provision were available (1983, 1985, 1986, 1988, 1991) and incorporating effects for hunting time, season day, and year, found no significant influence of hunting time on the decision of whether or not to add a second caterpillar to a nest (coefficient for hunting time: 0.00013 ± 0.00047 (SE), $P = 0.78$; Appendix S3, Fig. S1). In 1988, the only year

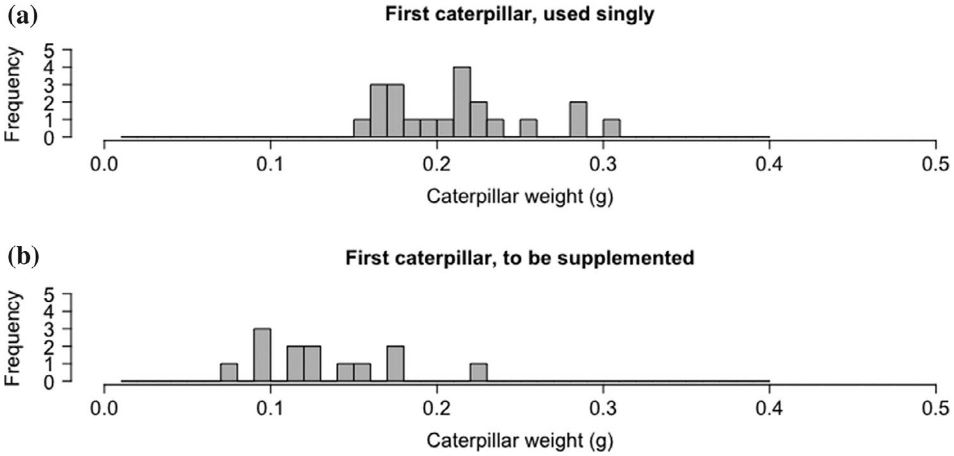

Fig. 1. 1988, fresh weights (g) of caterpillars provisioned by *A. dysmica*. (a) First caterpillar added to nests that immediately received a final closure, and thus were to be used as the sole provisions. (b) First caterpillar added to nests that immediately received a temporary closure, and thus were intended to receive additional caterpillar provisions. Effect of caterpillar weight on provisioning decision, coefficient for weight: −96.6 ± 38.6 (SE), $P = 0.012$ (File S1).

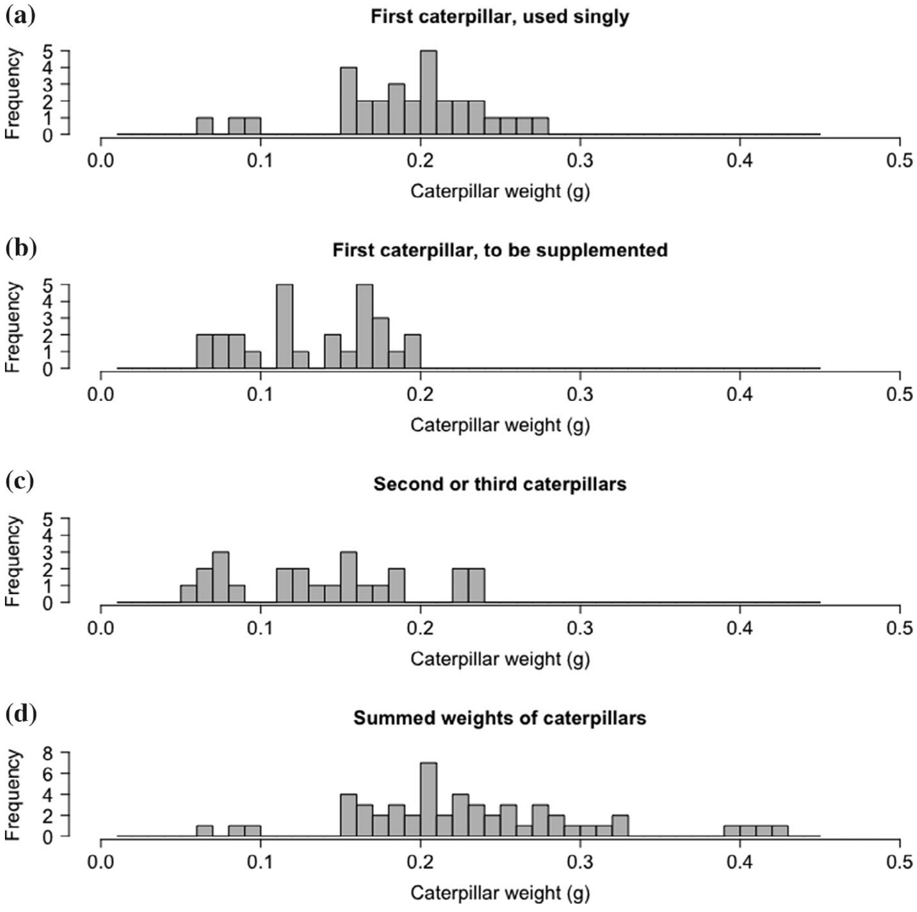

Fig. 2. 1991, fresh weights (g) of caterpillars provisioned by *A. dysmica*. (a) First caterpillar added to nests that did not receive additional provisions. (b) First caterpillar added to nests that received one or two additional caterpillar provisions. (c) Caterpillars added subsequently to nests that had already received an initial caterpillar provision. (d) Summed weight of all caterpillars (1, 2, or 3) added to completed nests.

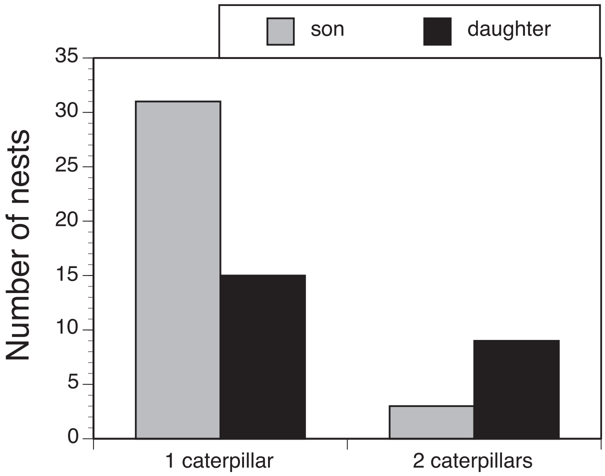

Fig. 3. Association between the number of caterpillars provisioned by *A. dysmica* and the sex of the offspring.

in which females were dissected immediately after making a provisioning decision, the length of the mother's largest maturing oocyte, and thus presumably her readiness to lay another egg, was uncorrelated with the mother's choice to add a second caterpillar to the nest (coefficient for egg load: 31.0 ± 16.0 (SE), $P = 0.053$; Appendix S1); the non-significant trend was in the direction opposite to that predicted by theory. Analyses that used an egg load metric that summed the lengths of the largest oocytes in each of the female's six ovarioles to obtain a more inclusive index of oocyte inventory showed no hint of an influence on nest provisioning (coefficient for egg load: 0.062 ± 1.46 (SE), $P = 0.97$).

Field observations suggest that *A. dysmica* in this population are able to mature eggs as fast or faster than they can capture caterpillar provisions for the resulting offspring, reducing the potential importance of egg limitation. Dissections of *A. dysmica* revealed that, immediately after laying one egg, virtually all individuals ($N = 35$) had another oocyte that was either fully mature or very nearly so (Fig. 4a). Deposited eggs were generally between 90 and 100% of the width of the female's head (Fig. 4b), and nearly all females had another developing oocyte of this size, or one only slightly smaller (length 80–90% of head width; Fig. 4a). Furthermore, caterpillar prey were consistently quite scarce, requiring females to spend on average close to a full day hunting to capture a single caterpillar; females are active from ca. 09:00–18:30 (9.5 h total) each day, and mean hunting times (hours ±1SE) were 7.37 ± 2.32 (1983, $n = 15$), 9.88 ± 0.78 (1986, $n = 107$), 9.30 ± 1.89 (1988, $n = 18$), and 8.77 ± 1.99 (1991, $n = 16$). Given that females that complete their provisioning of a nest must, at a minimum, close the nest, select a new nest site, excavate a new nest, and secure a caterpillar provision before they will have their next opportunity to oviposit, it may be that, in this population, the risk of not having a mature oocyte to lay is very small. Consistent with this inference was the observation that a female's hunting time for an initial caterpillar was uncorrelated with the female's residual egg load (length of largest remaining oocyte) immediately after ovipositing on the captured caterpillar (GLM, coefficient for hunting time, 0.000035 ± 0.000051, $t = 0.675$, $P = 0.51$). Even females who were lucky enough to capture a caterpillar after very short hunts still had sufficient oocytes to lay an egg and have a second mature or nearly mature oocyte remaining in their ovaries. In sum, I saw no evidence that *A. dysmica* reproduction was constrained by the availability of mature oocytes.

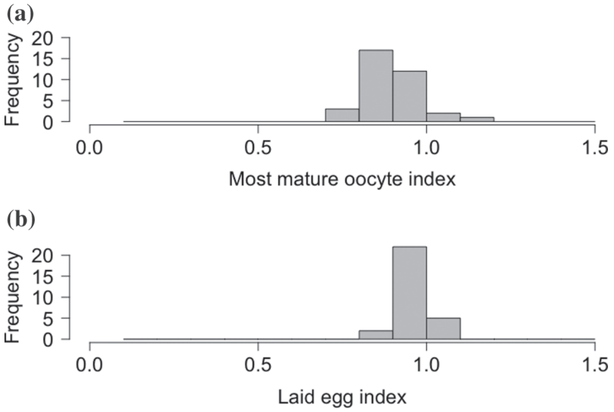

Fig. 4. *Ammophila dysmica* distribution of lengths of (a) the most mature oocyte remaining in the ovaries immediately following oviposition, and (b) the egg laid on the first provisioned caterpillar. Oocyte and egg lengths are divided by female head width to standardize for variation in female size.

Parasites

The risks that a parasite, mostly *A. armilla* but also occasionally *H. hilarella*, would penetrate the nest during provisioning did not appear to differ between the first and second provisionings of a nest (asymptotic Generalised Cochran–Mantel–Haenszel test, stratified by year, $\chi^2 = 0.191$, df = 1, $P = 0.66$; Fig. 5a). Given this, it seemed reasonable to expect that nests that were provisioned with two caterpillars, and which were therefore exposed to two windows of vulnerability rather than one, would incur a higher total risk of parasitism than would nests provisioned singly. Indeed, if I assume that parasite oviposition during the first and second provisionings are independent events, I can calculate an expected overall parasitism rate of 56.4% for 2-caterpillar nests (Appendix S4). It was, therefore, somewhat paradoxical to find that parasitism rates were no greater for nests receiving two caterpillars (29.7%) than for nests receiving only one (33.7%; asymptotic Generalised Cochran–Mantel–Haenszel test, stratified by year, $\chi^2 = 0.156$, df = 1, $P = 0.69$; Fig. 5b). This paradox was resolved, however, by the finding that *A. dysmica* females were significantly less likely to add a second caterpillar to nests that had been penetrated by parasites during the first provisioning (asymptotic Generalised Cochran–Mantel–Haenszel test, stratified by year, $\chi^2 = 4.58$, df = 1, $P = 0.032$; Fig. 5c). This contrast between subsequent provisioning of nests that were, or were not, penetrated by parasites during the first provisioning (Fig. 5c) demonstrates that *A. dysmica* truncates its investment in nests that have elevated risks of parasitism. The result is

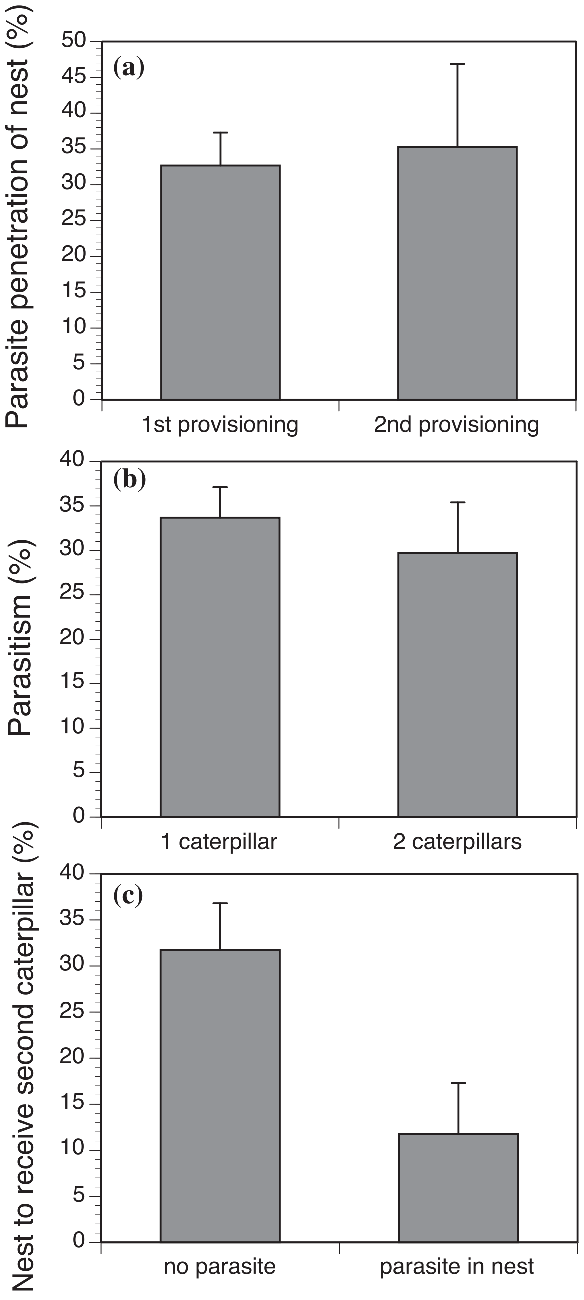

Fig. 5. Interactions of *A. dysmica* with its parasites. (a) Parasites are similarly likely to penetrate *A. dysmica* nests during the first provisioning (34/104 = 32.7%) as during the second nest provisioning (6/17 = 35.3%). (b) Parasitism rates of *A. dysmica* nests receiving a single caterpillar provision (64/190 = 33.7%) and nests receiving two caterpillar provisions (19/64 = 29.7%) are not significantly different. (c) Parasite penetration of the nest during the first provisioning reduces the likelihood that females will decide to add a second caterpillar provision to the nest. *Ammophila dysmica* chose to add a second caterpillar to 31.8% of nests (27/85) where parasites did not enter the nest during the first provisioning, whereas when parasites penetrated the nest, host wasps chose to add a second caterpillar only 11.8% of the time (4/34 nests). Each panel shows the means ±1SE (SE calculated assuming binomial distribution of the probability of adding a second provision).

that the burden of parasitism is effectively concentrated in singly-provisioned nests.

Because these are observational, rather than experimental, results, we need to consider the possibility that instead of parasite presence causing a change in provisioning decisions, causality could flow in the reverse direction, with some aspect of single caterpillar provisioning enhancing the vulnerability of the nest to parasites. One possible hypothesis is that the larger caterpillars that are generally used in singly-provisioned nests (Figs. 1 and 2) might be more conspicuous to parasites. I tested this hypothesis using data on caterpillar weights from 1988 and 1991, and found no effect of caterpillar size on the likelihood that parasites penetrate the nest during the first provisioning (GLM with main effects for caterpillar weight, season day, and year: coefficient for caterpillar weight: 12.1 ± 8.7 (SE), $N = 27$, $P = 0.16$).

A second result that helps to establish the plausibility of the interpretation that causality flows from parasite presence to altered nest provisioning decisions is that female *A. dysmica* revealed, in at least some cases, that they had detected the presence of parasites during nest provisioning. Across all years, in 19 of 31 (61.3%) of first provisionings in which parasites penetrated the nest, host wasps showed that they had detected the parasites, usually by attacking the parasites directly or, in some cases, by interrupting other activities to initiate rapid cleaning of the nest. I do not know if *A. dysmica* detected parasites in some of the remaining 12 cases without making an obvious display of this recognition. Nest excavations showed that nests penetrated by *A. armilla* during the first provisioning were almost invariably parasitised (23 of 24 cases, 95.8%). The detection of *A. armilla* parasites around the nest by *A. dysmica* did not, however, always reflect parasite oviposition in the nest: in 10 of 70 (14.3%) initial provisionings in which parasites did not penetrate the cell, *A. dysmica* still exhibited their awareness of parasite presence, typically by chasing them away from the nest entrance. There were 4 unusual cases out of a total of 34 nests where *A. dysmica* added a second caterpillar to a nest that was penetrated by a parasite during the first provisioning (Fig. 5c); in 3 of these 4 cases, the female's behaviour revealed that she had detected the parasite during the initial provisioning. Thus, *A. dysmica* routinely detected nest parasites, opening for them the opportunity to adopt a strategy of nest provisioning conditioned on parasite presence, but *A. dysmica* may still be uncertain about whether or not the nest has actually been parasitised.

The decision not to add a second caterpillar to nests that were penetrated by parasites during the first provisioning did not appear to represent simple nest abandonment: for 24 of 30 such cases, *A. dysmica* constructed full final nest closures, including the organic layer, a process that requires ca. 30 min of activity (Rosenheim, 1987a), and in the remaining 6 cases, at least a firm-packed closure was placed on the nest, requiring ca. 10 min of activity. Nests that were abandoned in other contexts (e.g., during the late stages of nest digging) never received firm-packed or full final closures, instead either being left open or, more often, being closed in a few seconds with a loose jumble of pebbles or other items. Thus, although *A. dysmica* appears to avoid making additional investments of caterpillar provisions in these high-risk nests, they nevertheless consistently invest in installing robust nest closures. This may reflect *A. dysmica*'s imperfect knowledge about whether or not a nest has actually been parasitised.

Discussion

Nest provisioning in *A. dysmica* appears to be highly flexible. Some ground-nesting wasps and bees construct cells of two sizes, larger cells for the offspring that will receive more provisions (often daughters) and smaller cells for offspring that will receive fewer provisions (often males; e.g., Brockmann & Grafen, 1989; Rooijakkers & Sommeijer, 2009). In contrast, *A. dysmica*, despite being sexually dimorphic, excavates cells of a single size class, irrespective of whether they will subsequently receive one or two caterpillar provisions. Thus, *A. dysmica* retains the ability to adjust nest provisioning in response to events surrounding the first provisioning. Like many solitary wasps, *A. dysmica* adjusts the number of provisioned prey to the size of each prey: when the first caterpillar provisioned is small, *A. dysmica* generally adds a second. Also like many solitary wasps and bees, *A. dysmica* is more likely to provide extra provisions, in this case a second caterpillar, to daughters. I found no support for the hypothesis that *A. dysmica* provisioning responded to the ease of capturing the first caterpillar (resource limitation) or the inventory of oocytes carried (egg limitation); mean hunting times were very long, and none of the females in our sample was without a mature, or very nearly mature, oocyte to lay even immediately following the laying of an egg. During roughly a third of all provisionings, parasites, mostly *A. armilla*, penetrated the nest; the risk of parasite invasion appeared to be the same for first and second provisionings of a nest. Surprisingly, however, nests receiving two caterpillars did not incur a greater total risk of parasitism. *Ammophila dysmica* detects parasite invasions during the first provisioning, and is much less likely to add a second caterpillar to invaded nests. Thus, *A. dysmica* effectively truncates its investment in nests associated with elevated parasitism risk.

Caterpillar size and number, and offspring sex

Ammophila dysmica's provisioning behaviour shares some features with that of its congener, *Ammophila sabulosa*, studied by Field (1992), but also differs in important ways. Field (1992) showed that *A. sabulosa* also provisions nests either with a single large caterpillar prey or with multiple, smaller prey. But *A. sabulosa* achieves an equal total weight of provisioned prey in singly- versus multiply-provisioned nests, whereas for *A. dysmica* multiply-provisioned nests receive a substantially larger total weight of caterpillars. Furthermore, Field (1992) found that *A. sabulosa* females appear to use a conditional hunting strategy: if the first caterpillar captured is small, females hunt for smaller caterpillars for subsequent provisions, suggesting that larger caterpillars were either rejected or, perhaps more likely, that females shifted to hunting locations where smaller prey were found. The caterpillars brought to nests by *A. dysmica* as second provisions may have been slightly smaller, on average, than caterpillars brought as first provisions, but the difference was small, and consequently two-caterpillar nests received about 50% more total provision weight than singly-provisioned nests. Thus, it was not surprising that two-caterpillar nests were primarily allocated to the production of daughters, which are ca. 1.57 times heavier than sons (Field *et al.*, 2015).

Prey limitation versus egg limitation

Solitary nest-building wasps and bees often produce heavily-yolked eggs that are large relative to the size of the adult female (Iwata, 1964; O'Neill, 1985; Rozen, 2003). Field *et al.* (2007) showed using a manipulative field experiment that the cost of a single egg made a significant contribution, equivalent to roughly half the cost of nest provisioning, to the overall cost of producing a single offspring in *Ammophila pubescens*, as reflected by a loss of future reproductive potential. Several researchers have suggested that when resources used to provision nests (pollen, prey) are abundant, the rate at which cells can be fully provisioned might outstrip the rate at which oocytes can be matured (Minckley *et al.*, 1994; Rosenheim *et al.*, 1996; O'Neill, 2001; Neff, 2008; Danforth *et al.*, 2019). Danforth (1989) studied a population of the communal bee *Perdita correopsidis* that appeared to exemplify exactly this situation: pollen was abundant on host plants located <5 m from the bees' nests, allowing bees to complete a foraging trip in an average of just 13.2 minutes and complete the provisioning of a cell with 6–8 such trips. As a result, female *P. correopsidis* could easily complete the provisioning of two cells per day, one in the morning and one in the afternoon. However, Danforth (1989) observed that some females, after completing a cell in the morning, simply rested during the afternoon, and dissections showed that these females lacked a mature oocyte. Other bees foraging under conditions of high pollen availability have been observed to exhibit similarly suggestive pauses in foraging behaviour, which have been interpreted as egg limitation (Minckley *et al.*, 1994; Neff, 2008). In contrast, *A. dysmica* appeared to face conditions of consistently low availability of caterpillars used as provisions, with a full day of hunting activity needed to capture a single caterpillar. As a result, each of the female *A. dysmica* ($N = 35$) that I dissected immediately after laying an egg still possessed an additional mature, or nearly mature, oocyte in her ovaries. Perhaps for this reason, *A. dysmica* showed no indication of adjusting its provisioning behaviour in response to either the hunting time needed to capture the first caterpillar or the female's egg load. Whether *A. dysmica* might exhibit plasticity of nest provisioning behaviour under conditions of greater caterpillar abundance remains an open question.

Costs incurred by parasites when they are detected by their hosts

Many parasites of solitary nest-building wasps and bees risk substantial losses of reproductive opportunities if they are detected by their hosts. In some cases, hosts can deploy defenses that prevent parasites from successfully ovipositing or

Fig. 6. *Ammophila sabulosa* chasing a chrysidid parasite *Hedychrum nobile* from the vicinity of its nest. This award-winning photograph was taken by Frank Deschandol in France in 2019. This parasite's hosts are other wasps, *Cerceris* spp. and *Odynerus* spp., but it was nonetheless pursued by this *A. sabulosa*.

larvipositing. For example, many ground-nesting wasps exhibit effective evasive flights when being trailed by parasitic flies that attempt to follow them as they return to their nests (Spofford *et al.*, 1986; Polidori, 2017). Hosts can also directly attack parasites, ejecting them from in, or near, the nest (Spofford & Kurczewski, 1992; Strohm *et al.*, 2008); for a dramatic example of a host wasp chasing a nest parasite captured by photographer Frank Deschandol, see Fig. 6). Host wasps and bees may also have effective defenses in response to actual parasite oviposition by direct destruction or removal of parasite eggs or larvae (e.g., Hager & Kurczewski, 1986; Spofford *et al.*, 1986; Torchio, 1989; Spofford & Kurczewski, 1992; Vinson *et al.*, 2011). Finally, for progressively provisioning *Ammophila* spp. wasps, which have extended contact between the mother and her developing offspring, as parasite larvae kill the host egg and begin to grow they reveal their presence to the host, which responds by abandoning the nest, thereby avoiding the costly process of bringing additional provisions to a nest that harbours only parasite offspring (Field & Brace, 2004).

Ammophila dysmica responds to the detection of *A. armilla* in or near the nest during provisioning with aggressive attacks. To avoid attacks, *A. armilla* often entered the nest during provisioning while the female was in the cell ovipositing or by following immediately behind the host wasp as it re-entered the nest after depositing soil removed from the nest on a cleaning trip. Like many chrysidids (Kimsey, 2006), *A. armilla* can, if attacked, roll into a defensive ball, displaying its heavily sclerotised and sculptured tergites to the attacking wasp. Nevertheless, *A. armilla*'s protection is not absolute. As noted by Strohm *et al.* (2008), the wings of chrysidids may still be vulnerable to damage by host attacks; one attack by *A. dysmica* on *A. armilla* rendered the parasite unable to fly (J. A. Rosenheim, unpubl. obs.). In one additional case, an *A. dysmica* exploited another structural vulnerability of its parasite: an *A. armilla* that had laid three eggs in the nest was captured by the host in the nest; the wasp emerged from its nest with the parasite in its mandibles, and over a 20 second attack fully severed the narrow junction of the parasite's mesosoma and metasoma, killing the adult parasite (J. A. Rosenheim, unpubl. obs.).

Ammophila dysmica responds to the detection of nest parasites during provisioning with increased efforts to clean the nest (Rosenheim, 1987a). Although such cleaning can eject newly deposited larvae of *H. hilarella* from the nest, it is entirely ineffective against *A. armilla*, which glues its eggs firmly to the caterpillar provisions or to the walls or ceiling of the cell (Rosenheim, 1987a). The current results show that *A. dysmica* also responds to the presence of parasites during provisioning by reducing its likelihood of adding a second caterpillar provision to the nest, thereby capping the resources available to the parasite's offspring. Unknown is whether the host wasp detects the adult parasite (using chemical, visual, or tactile cues), chemical traces left by the adult parasite in the nest, or the parasite's eggs. Regardless, it appears that *A. dysmica* is often aware of the parasite's presence, in contrast to other chrysidid wasps that use chemical mimicry to evade host detection in the nest almost entirely (Strohm *et al.*, 2008; Wurdack *et al.*, 2015).

Although *A. dysmica* reduces its likelihood of adding a second caterpillar to nests that were penetrated by parasites during the first provisioning, it does, on rare occasions, still do so, and it always works to place a secure, final closure on the nest, even when it detects parasites. I interpret these additional investments in the nest as a reflection of the host wasp's uncertainty regarding the status (parasitised versus unparasitised) of the nest. *Ammophila dysmica* often become aware of parasites that penetrate the nest during provisioning, but host wasps also often encounter and attack parasites that are present during provisioning but that never penetrate the nest. Thus, the host wasp appears to have only imperfect information regarding the fate of the nest, and therefore continues to invest enough to secure the success of the offspring if the nest has escaped parasite attack.

Conclusion

Ammophila dysmica nest provisioning behaviour appears to respond to information gathered at the first nest provisioning: the size of the captured caterpillar, the sex of the egg laid, and the magnitude of risk posed by nest parasites. By retaining substantial flexibility of provisioning, the host wasp appears to reduce its likelihood of committing extensive resources to nests that will only produce parasite offspring.

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Data availability statement

The data upon which this study is based will be archived at DRYAD upon acceptance of the manuscript.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Generalized Linear Model of factors associated with nest provisioning behavior in *A. dysmica*, 1988: effects of egg load and the weight of the first caterpillar provisioned.

Appendix S2. Generalized Linear Model of factors associated with nest provisioning behavior in *A. dysmica*, 1991: effects of the weight of the first caterpillar provisioned.

Appendix S3. Generalized Linear Model of factors associated with nest provisioning behavior in *A. dysmica*, 1983, 1985, 1986, 1988, and 1991: effects of the hunting time required to secure the first caterpillar provisioned.

Appendix S4. Calculating an expected likelihood that an *A. dysmica* nest that receives two caterpillar provisions will be penetrated by a parasite during either the first or second provisionings, under the assumption that parasite penetration during the first and second provisionings are independent events.

Fig. S1. Distributions of hunting times (hours) for the nest's first caterpillar provision for nests that received just a single caterpillar (top panel) and nests that received 2, or rarely 3, caterpillars (bottom panel).

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