Costs of egg-laying and offspring provisioning: multifaceted parental investment in a digger wasp

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Nest-building Hymenoptera have been a major testing ground for theories of parental investment and sex allocation. Investment has usually been estimated by the likely costs of offspring provisioning, ignoring other aspects of parental care. Using three experimental treatments, we estimated the costs of egg-laying and provisioning separately under field conditions in a digger wasp *Ammophila pubescens*. In one treatment, we increased the provisioning effort required per offspring by removing alternate prey items as they were brought to the nest. In two other treatments, we reduced parental effort by either preventing females from provisioning alternate nests or preventing them from both ovipositing and provisioning. Our results indicate that both egg-laying and provisioning represent significant costs of reproduction, expressed as differences in productivity but not survival. A trade-off-based model suggests that other components of parental care such as nest initiation may also represent significant costs. Costs of egg production and nest initiation are probably similar for male and female offspring, so that taking them into account leads to a less male-biased expected sex ratio. Mothers compensated only partially for prey removal in terms of the total provisions they gave to individual offspring.

Keywords: parental investment; parental care; sex ratio; provisioning; costs of reproduction; Hymenoptera

1. INTRODUCTION

Trivers (1972) defined parental investment as investment in offspring that occurs at the expense of parental ability to invest in future offspring. Organisms are expected to have evolved to balance their level of investment in individual offspring against the costs involved, so as to maximize their lifetime reproductive success (Williams 1966). Understanding the form that reproductive costs take is therefore critical to understanding investment decisions. In birds, it was long assumed that offspring provisioning is the costliest aspect of parental care, but this has recently been challenged through the finding that incubation and egg production also have substantial costs (Monaghan *et al.* 1998; Visser & Lessells 2001). Nest-building Hymenoptera have been a major testing ground for theories of parental investment and sex allocation (e.g. Trivers & Hare 1976; Seger 1983; Boomsma & Grafen 1990). Investment has usually been estimated by the likely costs of provisioning: total mass of provisions provided; or mass of adult offspring themselves (e.g. Trivers & Hare 1976; Field 1992; Helms 1994; Strohm & Linsenmair 1999). Female offspring usually require more provisions than males, so that a male-biased numerical sex ratio is then expected under Fisher's (1930) theory of equal investment. However, such calculations ignore aspects of parental care other than provisioning, such as nest-building, egg production and the guarding of immatures. In reality, investment is likely to be 'multifaceted', more than one component of care will be costly. Sex allocation and the level of investment in individual offspring should then depend on the relative costs of the different

components of care (Rosenheim *et al.* 1996). For example, if egg production rather than provisioning was the major cost of reproduction, then the predicted sex ratio would approach 1 : 1, since male and female eggs usually differ only in whether they are fertilized (Rosenheim *et al.* 1996).

In this paper, we make the first direct comparison between the costs of provisioning and the costs of egg-laying in a hymenopteran. In unmanipulated populations, correlations between life-history traits are often positive; better-resourced females might not only lay more eggs, but also provide more provisions per egg. In order to estimate reproductive costs, experimental manipulation of effort is therefore necessary (Partridge & Harvey 1988; Lessells 1991). We manipulated costs either by causing offspring to require more of a particular component of care than would usually be the case or by preventing parents from performing that component. If the component of care is costly in the sense of Trivers (1972), increased performance should reduce a parent's lifetime number of offspring, whereas reduced performance should increase that number.

2. MATERIAL AND METHODS

(a) Study species

Ammophila pubescens Curtis (Sphecidae) is a digger wasp that nests on open sand within heather-dominated heathland. Females (length 1.5–2 cm) nest alone and place each offspring in a separate burrow, which is kept closed when the mother is away. Mothers provision their offspring with lepidopteran caterpillars, which they paralyse by stinging and then transport to the burrow in flight or (with larger prey) by dragging. *Ammophila pubescens* is a progressive provisioner, i.e. each offspring is fed gradually as it grows (Baerends 1941;

Field & Brace 2004; Field 2005). A typical nesting sequence in our study population proceeds as follows. On day 1, a female digs a short burrow ending in a horizontal cell. Later that day, or on day 2, she places one caterpillar in the cell and lays a single egg on it. No further provisioning then occurs for approximately 5 (range 2–8) days, during which the egg hatches and the larva feeds on the caterpillar. During this time, the mother enters the burrow and assesses the needs of her larva (Baerends 1941). She may also initiate and provision other burrows, and normally has two to four separate burrows in mid-provisioning at a time (J. Field & W. A. Foster 2004, unpublished data; Baerends 1941). Around day 6, the mother begins the 'main provisioning bout', in which she adds 8 ± 0.6 (mean $\pm$ s.e., range 5–15) further caterpillars over a period of typically 1–2 (range 1–7) days. In approximately 30% of cases, the mother interrupts the main provisioning bout to dig or provision another burrow. At the end of the main provisioning bout, the mother permanently closes the burrow. The larva consumes the caterpillars then pupates in the cell. The different burrows initiated by one female are normally placed within a few metres of each other. Temperatures above 18–19°C are required for nesting activity, and males are not involved in nesting.

Females in our population sometimes enter burrows dug by other females, sometimes ejecting caterpillars and the wasp immature. The entering female often then provisions the burrow over one or more days, as does the female that dug the burrow ('joint provisioning'). Approximately 10% of burrows are joint-provisioned, by up to five different females each. An enterer probably replaces the egg that she finds with her own egg, and it is unlikely that more than one larva can develop in the same burrow (Field 1989a). Individual females provision both burrows that they have dug themselves and burrows dug by other females.

(b) Manipulation of provisioning effort in 2004

In 2004, we estimated the costs of offspring provisioning by either increasing or decreasing the amount of provisioning required per offspring. We had a relatively small observation area, allowing us to record behaviour in detail. Our study was conducted at Thursley Common, Surrey, UK, where *A. pubescens* nests between mid-June and late August. In 2004, the first month after female emergence was rainy and cool, with very little nesting activity. During this time, we individually marked females within our focal observation area, a 6.5×1.6 m length of sandy path. Forewing length was measured using digital callipers. Our experiment ran from 21 July until 11 August, the first sustained period of warm weather after female emergence. Females were divided into three treatment groups after blocking for wing length: increased provisioning effort per offspring (IP); reduced provisioning effort per offspring (RP); and unmanipulated controls. The IP treatment was to remove every other prey item from each female as she arrived at her burrows. Each prey was removed after the female had dropped it next to a burrow and was preoccupied reopening the burrow. The IP treatment period ran from 21 July to 1 August (12 days). If provisioning is costly and females replace prey that are removed, our directional hypothesis is that IP females will produce fewer burrows than controls, owing to the increased provisioning effort that each burrow requires (one-tailed test).

The RP treatment was to destroy every other burrow that a female dug, starting with the first one. The RP treatment period ran from 21 July to 11 August (22 days). Burrows were

destroyed on the evening of the day they received their first prey item and egg, by obliterating the entrance then covering it with a flat stone. At her next visit, the female would investigate the stone before permanently abandoning the nest. At every other burrow she dug, an RP female thus laid her egg but provisioned only the first prey item. If provisioning is costly, our directional hypothesis is that RP females will produce more burrows than controls, owing to their reduced provisioning effort per burrow (one-tailed test). We compared RP and control females from the point when each female dug her first burrow (first burrow date) until the end of the RP treatment period. First burrow date did not differ between RP (mean 25 July) and control (mean 26 July) females. Two females that failed to dig any burrows were excluded from analysis.

During the IP treatment period, two observers watched the focal observation area throughout the activity period each day (08.30–18.00 h), and periodically scanned a 5 m peripheral area on each side. We recorded every time a marked female dug a new burrow or brought a prey item to an existing burrow (provisioning). Burrows were permanently marked. Prey items were categorized as 'small' or 'large' based on their size relative to female wasps. Among prey that we removed from IP females, those classified as large were significantly heavier than those classified as small (0.052 ± 0.007 g, $n = 36$ and 0.014 ± 0.002 g, $n = 38$, respectively, Wilcoxon test, $p < 0.0001$). After the IP treatment period ended (1 August), only burrow digging was recorded until 11 August when the RP treatment ended. Of the original 46 marked females, four were excluded from analysis because they did not nest in our observation area or we confused their colour marks. The remaining females were never seen nesting outside the area monitored, despite searches of adjacent areas.

As noted earlier, *A. pubescens* females sometimes provision foreign burrows. Females might find foreign burrows by chance, while searching for somewhere to dig (Field 1989b). Since we were expecting RP females to dig more burrows than controls, costs of provisioning that they avoided owing to our manipulation could be expressed as an extra investment in foreign burrows. We therefore compared the number of burrows that RP and control females joint-provisioned after their first burrow dates, excluding burrows that they were known to have dug themselves. Approximately half of these joint-provisioned burrows had been dug by unidentified females before the start of our observations.

Provisioning events often last only 10–20 s, and these could be missed when they occurred in the 5 m peripheral areas. When analysing the number of prey captured under different treatments, we therefore included only females that nested exclusively within the focal area or (when analysing the number of prey placed in individual burrows) only burrows situated within that area. In contrast, burrow digging lasts at least 1 h and is highly visible; when analysing the number of burrows produced, we included all females. In all comparisons between treatments, we tested the significance of female wing length as a covariate, since larger females might have more resources to devote to offspring.

(c) Manipulation of reproductive effort in 2005

In 2005, we manipulated parental effort in a larger number of individuals over most or all of their lifespans. We applied three treatments. Two of them were control and RP, as in 2004. The third treatment was similar to RP, except that alternate burrows were destroyed immediately after digging, before

oviposition could occur. Females in this reduced provisioning effort-reduced oviposition (RPO) treatment not only provisioned only half of the burrows they dug, but also oviposited in only half.

Our focal observation area was a 70×2 m length of sandy path, well separated from the path used in 2004. During 22–27 June, when females were in mid-emergence, we marked 179 females that eventually nested in the focal area and became a part of the experiment. Some females began nesting during the marking period, before our experiment could begin, but because treatments were assigned randomly, such females should have been divided approximately evenly between the treatments. Treatments and monitoring began on 27 June. Whenever conditions were suitable for nesting activity, two or three observers walked continuously along the focal 70 m of path plus 8 m each side, recording and marking all burrows being dug. The experiment continued until 8 August, by which time marked females had almost completely disappeared. Censuses on 11, 19 and 30 August revealed only three, one and zero marked females, respectively.

During the experiment, we destroyed 51% of burrows dug by RP females and 50% dug by RPO females (1.41±0.09 and 1.55±0.11 burrows per female, respectively). The RP burrows were destroyed on the evening of the day after digging, to allow time for oviposition to occur. Extra time was allowed after inclement weather. Examination of cell contents showed that 88% of destroyed RP burrows were destroyed after oviposition as intended and 98% of destroyed RPO burrows were destroyed before oviposition.

In 2005, we tested whether treatment affected two components of reproductive success tied closely to fitness: the total number of burrows produced; and female survivorship. If both egg production and provisioning are costly, then our directional hypothesis is that RPO females will produce more burrows than RP females, which in turn will produce more burrows than controls. We used a one-tailed, ordered heterogeneity test (Rice & Gaines 1994), which takes into account both the magnitude of any difference between treatments (the *p*-value from ANOVA) and the extent of any trend across treatment means in the predicted direction (Spearman's rank correlation coefficient). The significance of wing length and first burrow date were tested as covariates. A later first burrow date probably reflected later adult emergence and/or mating. Since first burrow date was significant as a covariate, we obtained Spearman's r_s by correlating treatment (coded in the order: controls; RP; RPO) with the mean residual number of burrows for each treatment from an ANOVA with only first burrow date fitted (see also Visser & Lessells 2001). Survival analysis was used to test whether treatment, wing length and first burrow date affected female survivorship, assuming that females died on the day they were last observed.

(d) Statistical analysis

Data were analysed using generalized linear modelling in the *R* statistical package, v. 2.0.0 for Macintosh (Crawley 2005). We began all analyses with all potential explanatory variables and interactions fitted. Starting with interaction terms, we then subtracted terms from the model until further removals led to significant ($p<0.05$) increases in deviance, as assessed from values of *F* with normal and Gamma errors or χ^2 with binomial and Poisson errors. We report significance levels for terms when adding them last to this minimal adequate model. Survivorship was analysed using the 'survival' package in *R*.
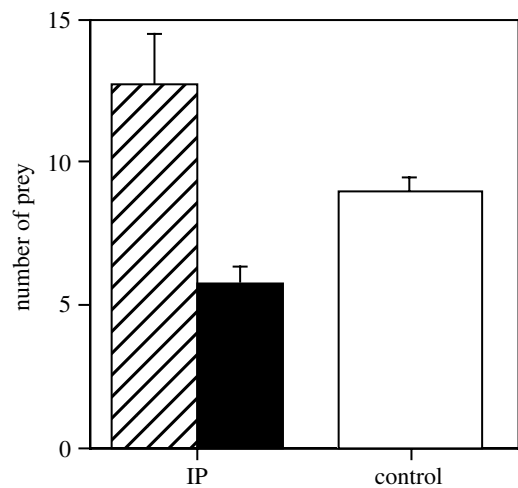

Figure 1. The mean number of prey caterpillars per burrow for IP ($n=11$ females) and control ($n=15$ females) treatments in 2004, based on 1.9±0.13 nests per female. The left-hand (hatched) bar for the IP treatment shows the total number of prey captured, whereas the right-hand (solid) bar shows the number provisioned after deducting prey that were experimentally removed. Joint-provisioned nests are excluded. Bars show 1 s.e.

In all analyses, data points are values or means for individual females and probability levels are for two-tailed tests unless otherwise stated. Mean±s.e. are quoted.

3. RESULTS

(a) The effect of increased provisioning effort in 2004

The IP treatment was successful, in that IP females brought 42% more prey to individual burrows than did control females (including prey that we removed, figure 1; $p=0.03$). As then expected, if provisioning is costly, IP females produced only 56% as many burrows as controls during the treatment period. This difference was significant when we included only females that nested exclusively within the focal observation area (one-tailed $p=0.029$, $n=7$ control and 9 IP females), or if we also included females that nested partially within the 5 m peripheral areas (figure 2a; one-tailed $p=0.018$). While we probably detected all burrows dug in peripheral areas, we could not have removed as large a proportion of prey from females nesting there.

As well as capturing more prey per burrow than controls, IP females captured significantly more prey in total over the entire IP treatment period (IP: 33.4±1.9, $n=9$ females; controls: 27.9±1.2, $n=7$; $p=0.03$). A possible explanation could be that IP females worked faster or longer hours than controls, but there was no evidence for this. There was no difference in the time when control and IP females were first recorded digging or provisioning each day, or the time when they were last recorded ($p>0.2$ in both cases, $n=7$ control and 9 IP females). The IP females had longer main provisioning bouts than controls because they captured more prey (including prey that we removed), but there was no evidence that the two sets of females captured prey at different rates ($y=$ the length of main provisioning bout; prey number: $p<0.0001$; treatment: $p=0.24$; $n=9$ IP and 12 control females, excluding bouts that were interrupted).

Whenever we removed the first prey item brought to a burrow by an IP female, she brought a replacement on which to oviposit. However, IP females did not fully compensate for prey that we removed. After deducting
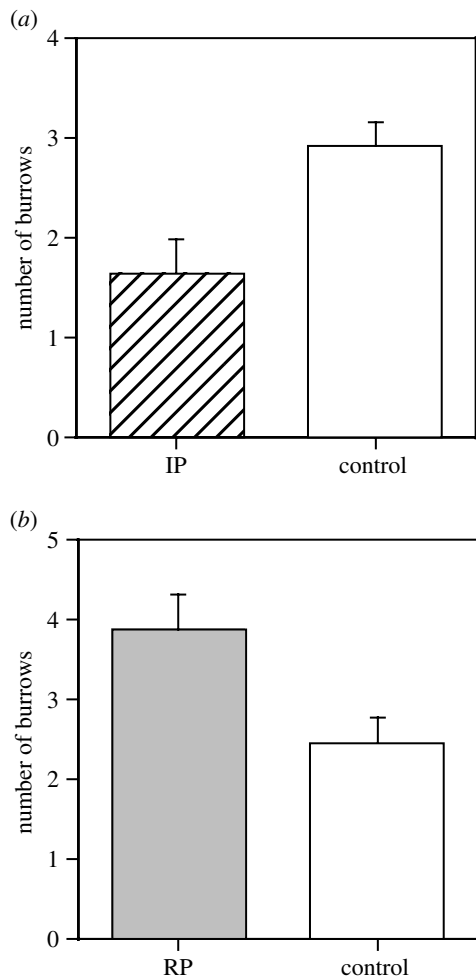
(a)

(b)

Figure 2. The mean number of offspring (burrows) produced by (a) IP ($n=14$) and control ($n=11$) females during the IP treatment period in 2004 and (b) RP ($n=15$) and control ($n=11$) treatment females in the period between each female digging her first burrow and the end of the RP treatment in 2004. Bars show 1 s.e.

prey that were removed, IP females provided individual offspring with significantly fewer prey than did controls (figure 1, $p=0.004$). A possible explanation for this could be that females responded to the treatment by laying more eggs of the sex requiring less food (males). However, this is unlikely, since the same pattern was evident at nests where the main provisioning bout occurred entirely during the treatment period, but oviposition itself had occurred before the treatment began, so that offspring sex was already determined. Considering only such burrows, IP females still provided fewer prey per offspring than controls ($p=0.04$, $n=8$ IP females and 8 controls). IP females also did not compensate for a smaller number of prey per offspring by using a larger proportion of large prey ($p=0.48$).

(b) *The effect of reduced provisioning effort in 2004*
Including their first burrows, RP females had 61% of their burrows destroyed after provisioning the first prey item. In response, RP females produced 57% more burrows than controls between their first burrow dates and the end of the treatment period (figure 2b; one-tailed $p=0.023$). The RP and control females provisioned similar total numbers of prey between their first burrow dates and the end of prey monitoring on 1 August (14.7 ± 2.7 and 14.6 ± 3.2, respectively, $p=0.2$). There was also no difference
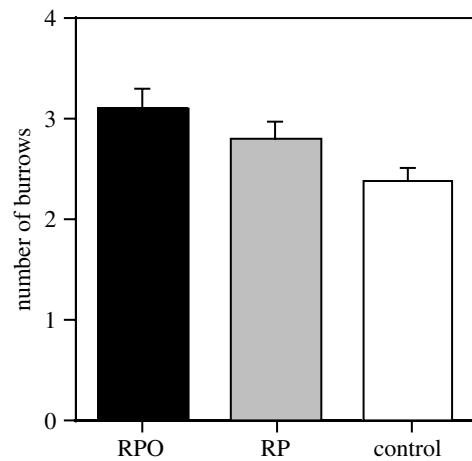
Figure 3. The mean number of offspring (burrows) produced by females in the RPO ($n=64$), RP ($n=61$) and control ($n=54$) treatments during the entire experimental period in 2005. Bars show 1 s.e.

between RP and control females in the proportion of their prey that were small (RP 0.52 ± 0.054; controls 0.49 ± 0.061; $p=0.11$), the number of prey they placed in individual unmanipulated burrows (RP 8.5 ± 1.1, $n=7$; controls 8.0 ± 0.7, $n=15$; $p>0.5$) or the number of joint-provisioned burrows (RP 0.67 ± 0.21; controls 0.18 ± 0.12; $p>0.3$ after controlling for first burrow date).

(c) *The effect of reduced provisioning effort and oviposition in 2005*
The number of burrows produced varied across treatments in the expected direction (figure 3). RPO females produced 31% more burrows than did the controls and RP females produced 18% more than the controls. Both treatment ($p=0.026$, figure 3) and first burrow date ($p<0.0001$) had significant effects on the total number of burrows. The overall ordered heterogeneity test produced significant support for our directional hypothesis ($r_s=1.0$, $P_c=0.974$, one-tailed $p<0.005$).

Female mortality rates were higher later in life, and analyses based on models such as the Weibull, which allow non-constant mortality rates, explained more of the variation than exponential models. However, whatever model was used there was no effect of treatment or female size on survivorship, but a significant effect of first burrow date ($p=0.01$); females that dug their first burrows late also died late.

4. DISCUSSION
We found that in *A. pubescens*, both oviposition and provisioning reduce a female's future productivity. Our 2005 results are the most complete, since we monitored all females until death. Females that did not have to oviposit in or provision alternate burrows (RPO) produced more burrows in total than females that oviposited but provisioned only the first prey item (RP), and these latter females, in turn, produced more burrows than controls, which both provisioned and oviposited normally (figure 3). There was no evidence that different components of parental care involve different ecological costs, such as risks of predation or parasitism, although larger sample sizes would be necessary to detect small differences in adult mortality rates. Assuming that costs are constant, additive and drawn

from a common resource pool, we can estimate the costs of different components of parental care as follows. In 2005, control females produced 2.37 ± 0.16 burrows (figure 3), so that their total resources spent on offspring (T_c) = $2.37E + 2.37P + 2.37N + F$, where F represents the costs that are independent of the number of offspring produced. E and P represent the costs of laying an egg and fully provisioning it, respectively, and N represents the sum of other costs, such as burrow construction. Analogous expressions for RP and RPO females are as follows

$$T_{RP} = 2.62 \pm 0.19E + 1.53 \pm 0.15P + 2.79 \pm 0.21N + F,$$
$$T_{RPO} = 1.58 \pm 0.16E + 1.55 \pm 0.16P + 3.09 \pm 0.22N + F.$$

These figures result because: (i) we manipulated only half of the burrows dug by RP and RPO females, (ii) 12% and 2% of manipulated RP and RPO burrows, respectively, were manipulated before or after oviposition, respectively, in error, and (iii) nests destroyed after oviposition but before the main provisioning bout still received the first of an average complement of nine prey items. Thus, for example, provisioning effort by RPO females is calculated as follows: $(3.094/2) + \{(3.094 \times 0.02)/(2 \times 9)\} = 1.55$ burrows-worth. Assuming that females in all treatments start with equal resources, set $T_{RP} = T_{RPO}$. After cancelling, we obtain $N = 3.394E - 0.068P$. Then setting $T_c = T_{RP}$, we obtain $0.84P = 0.25E + 0.417N$. Substituting for N, we obtain $P = 1.9E$ and $N = 3.3E$, so that costs are estimated to be in the ratio $1 : 1.9 : 3.3$ ($E : P : N$). Under this trade-off-based model of resource allocation, our results imply that provisioning an egg is roughly twice as costly as laying it, and that other aspects of parental care such as nest construction comprise half of the total costs of offspring production. While we do not wish to overemphasize these precise figures, it is conceivable that nest-building and finding a burrowing site are energetically very costly in *Ammophila*. They often occur at high temperatures, and nest construction involves more than 1 h of intensive digging, during which soil is loosened using body vibrations then carried into the air and dropped (Field 1989*b*; see also Brockmann 1979). If provisioning was the only cost of offspring production, then RP and RPO females would have paid approximately 50% of the costs paid by controls, and they should therefore have been able to produce twice as many burrows (cf. figure 3).

Our results from 2004 corroborate the finding that provisioning is costly; increasing or decreasing the provisioning effort required per offspring led to a decrease or increase, respectively, in the number of burrows produced (figure 2). We cannot calculate cost ratios in the same way as with our 2005 data, because there was no RPO treatment in 2004. RP females produced only 57% more burrows than controls in 2004, again implying that provisioning is not the only cost of reproduction. However, a 57% difference is considerably greater than the 18% difference in 2005. This could imply that provisioning was more costly in 2004, for example if prey were scarcer. However, our 2004 data are less reliable because samples were much smaller than in 2005, and because we measured burrow production during only part of the lifespan. The 2004 results are consistent with an assumption we made in calculating costs from our large-scale 2005 experiment, that parental effort differed between treatments in terms of only the components we manipulated. Our detailed data from 2004 show that the

total number of prey provided for unmanipulated offspring, and the size of individual prey, did not differ between RP and control females. In addition, there was no evidence that RP females joint-provisioned more foreign burrows than did controls. Since RP females dug more burrows than controls, this suggests that in *A. pubescens*, foreign burrows may not always be found opportunistically during the search for digging sites.

In addition to bringing more prey to each burrow, IP females from which alternate prey were removed captured 20% more prey in total than controls over the 12-day treatment period. There was no evidence that IP females worked harder than controls to compensate for prey removal, although sample sizes were small. A simple hypothesis consistent with our data is that prey removal prolonged provisioning at individual burrows, so that fewer new burrows could be dug.

After subtracting prey that we removed, IP females compensated only partially in terms of the amount of food they provided for individual offspring (figure 1). It is unlikely that this resulted from a switch to producing offspring of the cheaper sex (males), but there are other possible explanations. One possible explanation is that mothers perceive prey removal as a reduction in prey availability. If prey become more limiting compared with other resources, a female risks dying before she can find enough food to provision all of her eggs, and it could be adaptive to provide less food per offspring (Rosenheim *et al.* 1996). A second possible explanation for incomplete compensation is that like many vertebrates, *A. pubescens* provisions more than one offspring simultaneously. Continuing to provision a particular offspring may therefore cause others to lose weight or even starve. The majority of wasps and bees instead provision only one offspring at a time, so that they do not have to adjust to this constraint (Field 2005).

Most previous studies of parental investment in nest-building Hymenoptera have measured costs involved only in provisioning: foraging for provisions; transporting them to the nest; and venom production in wasps (e.g. Trivers & Hare 1976; Field 1992; Helms 1994; Strohm & Linsenmair 1999). A few studies have considered brood cell volume as a measure of cost (e.g. Trivers & Hare 1976; Helms 1994). Our finding that oviposition and nest initiation are also costly suggests that provision weight and offspring size do not, on their own, fully capture parental investment. Compared with parasitoids, nest-building wasps and bees tend to have low fecundity and large eggs that may be costly to produce (Rosenheim *et al.* 1996; O'Neill 2001). Because we manipulated oviposition opportunities rather than egg production *per se*, our experiment may even have underestimated the costs of egg-laying if some RPO females had to recycle mature eggs following burrow destruction. Recycling could be inefficient, so that females would not then have avoided the full costs of egg production. Taking egg-laying costs into account leads to a less male-biased expected sex ratio than would be the case if only provisioning costs are considered (Rosenheim *et al.* 1996). Like egg-laying costs, the costs of searching for a burrowing site and some of the costs of nest-building, such as the effort required to dig the main shaft of an *Ammophila* burrow, are probably the same for both sexes of offspring. In contrast, female-producing cells are usually larger than male-producing cells in wasps and bees, reflecting the larger

mass of prey that must be stored to feed a female larva (e.g. Trivers & Hare 1976; Field 1992; Helms 1994; Strohm & Linsenmair 1999).

Attempts to measure the costs of different components of parental care in invertebrates have had mixed results. Tallamy & Denno (1982) showed that maternal guarding of eggs and immature offspring reduced the lifetime fecundity of tingid bugs (Hemiptera). However, despite large sample sizes, Agrawal *et al.* (2005) failed to detect any costs of egg-guarding or offspring provisioning in cydnid bugs in the laboratory. Both egg-guarding and provisioning were costly in a subsocial spider (Gundermann *et al.* 1997). Strohm & Marliani (2002) attempted a manipulation of laboratory hunting effort in the digger wasp *Philanthus triangulum*. In one experiment, they provided a set of females with prey ad libitum, while another set were each restricted to only one prey per day throughout their lives. The restricted set captured less than half the number of prey per day of the ad libitum set, yet the restricted set had marginally shorter, not longer, lifespans. This result is doubly surprising because in addition to capturing fewer prey, restricted females would presumably have been able to lay fewer eggs and dig fewer nest cells than females in the ad libitum treatment (see Strohm & Linsenmair 1997). The methodology used may account for these unexpected results, and other experiments did suggest that there was at least a short-term cost of provisioning (Strohm & Marliani 2002).

Nest-building wasps and bees are unusually promising taxa among which to compare the costs of different components of parental care under the field conditions where results are most meaningful. Their diverse natural histories suggest that there may be considerable inter-specific variation in the relative magnitude of these costs (e.g. Michener 2000; O'Neill 2001). While some species nest in pre-existing cavities such as hollow plant stems, others must carry out potentially costly nest excavation *de novo* in soil or rotting wood, or construct nests using material gathered from the external environment. In some taxa, prey capture requires the production of potentially costly venom, while in bees and some wasps this is not the case. There is also considerable interspecific variation in egg size relative to body size (e.g. Iwata 1964; O'Neill 2001). Our study has shown that egg-laying, provisioning and probably also nest initiation can represent significant costs of offspring production. Further studies of the costs of reproduction in nest-building wasps and bees, including comparative studies, should be extremely profitable.

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