

# The evolution of progressive provisioning

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Most nonsocial wasps and bees are mass provisioners (MP), sealing each egg into its own cell containing all of the food required to reach maturity. Other species instead provision progressively, feeding their offspring only gradually as they develop and usually provisioning more than one offspring simultaneously (SPP). The evolution of progressive provisioning is interesting because it has obvious drawbacks. In particular, it could prolong the period of offspring dependency, and hence increase the chance that a mother will die before her offspring reach independence. Prolonged dependency could in turn facilitate the evolution of helping through insurance-based mechanisms. In this paper, I outline two ecologically extreme models of how reproductive success is accrued during provisioning. In Model 1, immature offspring become independent as soon as they are fully provisioned. SPP is then disadvantageous because it prolongs the provisioning period compared with MP. If SPP does evolve, Model 1 predicts that brood size, the number of offspring provisioned simultaneously in a batch, should be minimized. Model 2 differs from Model 1 in that offspring become independent only at adulthood. SPP can then be advantageous because investment is converted into independent offspring more quickly than under MP. Model 2 predicts an intermediate brood size, positively correlated with larval development time and the abundance of provisions. *Ammophiline digger wasps and eusocial vespids may correspond to Models 1 and 2, respectively, whereas ground-nesting wasps and bees with multicellular nests may be intermediate.* *Key words:* eusociality, insurance, parental care, progressive provisioning, wasps. [*Behav Ecol* 16:770–778 (2005)]

The immature offspring of nest-building wasps and bees, like the offspring of many vertebrates, are helpless and rely entirely on adult carers to provide them with food. Unlike vertebrates, however, most wasps and bees are so-called “mass provisioners:” each egg is sealed into a cell containing all the food required for maturation, so that within 1–2 days of oviposition the offspring is nutritionally independent of its mother. In contrast, a minority of wasps and bees exhibit a form of extended parental care known as “progressive provisioning.” In these, the mother provides only a small amount of food, or no food, before the egg hatches, and provisions each developing larva gradually as it grows, over a period that can range from approximately 7 to 70 days. Mass provisioners include the vast majority of nonsocial wasps and bees, plus eusocial bees in the families Halictidae (sweat bees), Xylocopidae (carpenter bees), and Meliponidae (stingless bees) (Bohart and Menke, 1976; Cowan, 1991; Michener, 2000). Progressive provisioners include a small proportion of nonsocial wasps in several phylogenetically separate genera, most or all eusocial bees in the subfamilies Allodapinae, Bombinae (bumblebees) and Apinae (honeybees), ants and all the eusocial vespid wasps (Stenogastrinae: hover wasps; Polistinae: paper wasps; Vespinae: yellowjackets) (Bohart and Menke, 1976; Cowan, 1991; Hunt, 1999; Michener, 2000).

Progressive provisioning is interesting in part because it appears to have two major drawbacks. The most obvious is that it could greatly reduce a mother's rate of offspring production. An individual mass provisioner typically fully provisions one to two offspring per day. By waiting for her larva to consume each feed before she provides the next feed, a progressive provisioner may instead require the full larval feeding period, at least 7–10 days, to fully provision each offspring (e.g., Baerends, 1941b; Evans, 1966). Most progressive provisioners, however, potentially avoid this disadvantage by

provisioning several offspring simultaneously: simultaneous progressive provisioning (SPP). It is SPP, the form found in most or all eusocial progressive provisioners, that I focus on here. The second disadvantage of progressive provisioning, detailed more thoroughly below, is that it potentially prolongs each offspring's period of dependency and hence increases the chance that a mother will die before her offspring reach independence.

In this paper, I investigate the conditions under which SPP could evolve by comparing its reproductive success with that of mass provisioning (MP) under different ecological conditions. Field and Brace (2004) show how the extended parental care inherent in progressive provisioning can significantly reduce costs incurred through interspecific parasitism. I first outline a model that shows how disadvantageous progressive provisioning can be through prolonging offspring dependency and hence how large a reduction in costs is required to outweigh that disadvantage. I then describe a second model in which progressive provisioning can provide mothers with a demographic advantage over mass provisioners under certain conditions. The models make contrasting predictions about brood size, the number of offspring provisioned simultaneously by a progressive provisioner.

As well as being of interest in its own right, progressive provisioning facilitates the evolution of other important traits, such as larva-adult communication and, in wasps, the provision of liquefied and divided prey items that would presumably rapidly rot if they could not be fed directly to larvae. Especially notable is how progressive provisioning might relate to mechanisms for the evolution of helping that rely on insurance (Gadagkar, 1990; Queller, 1994, 1996; Reeve, 1991). When a lone mother dies, any offspring that she has provisioned only partially are likely to starve. In contrast, a helper in a eusocial group has a form of insurance: after she dies, offspring that she has only partially reared can be brought to adulthood by her surviving nest mates (Field et al., 2000; Shreeves et al., 2003). The longer the period of offspring dependency, the smaller the chance that a lone mother will live long enough to bring her offspring to independence. Through prolonging the period of dependency

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without altering maternal lifespan, progressive provisioning could therefore increase the insurance-based advantage to potential helpers. This would make concrete the link, often implied by previous authors, between progressive provisioning and the evolution of helping (Hunt, 1999; Schwarz et al., 2003). Helpers in facultatively eusocial wasps certainly benefit through insurance-based advantages (Field et al., 2000; Shreeves et al., 2003), but whether such advantages operated to the same extent at the origin of helping is more questionable (but see Queller, 1994, 1996). This would require prolonged dependency to have evolved before helping in ancestral nonsocial species, when it would leave dependent offspring with only a single, short-lived carer. The analysis below, by revealing the conditions under which progressive provisioning will be favored by natural selection, could indicate how likely a scenario this is.

## METHODS

Parameters used in the models are listed in Table 1. I focus on independent-nesting mothers because I am particularly interested in how prolonged dependency could evolve before helping, but the same kinds of arguments could be applied to the evolution of progressive provisioning in social species. The models require estimates of the mortality rates of mothers. For two nonsocial digger wasps (Sphecidae), field mortality estimates are in the range 0.01–0.07/day (Freeman, 1980; Toft, 1987). In many eusocial wasps, nests are founded by single females that remain alone until offspring (worker) emergence. Queller (1996) compiled data from 19 field studies of polistine wasps, giving the proportion of lone foundresses that survive until worker emergence. Assuming a constant mortality rate and offspring development periods of 40–50 days, these data again imply daily mortality rates in the range 0.01–0.07. Finally, in a stenogastrine wasp, the adult mortality rate of lone females was 0.015/day (Field et al., 2000). Given these data, in this paper I focus on daily mortality rates in the range 0.01–0.1.

### Model 1: offspring become independent when they are fully provisioned

Model 1 assumes that mothers do not visit or guard their offspring once provisioning is complete, so that fully provisioned but immature offspring are independent, that is, unaffected by their mother's death. Model 1 corresponds to certain nonsocial digger wasps such as the genus *Ammophila*, in which each offspring is placed in a spatially separate short burrow in the ground. In mass provisioners (MP) species, the mother provisions a burrow with one or several paralyzed caterpillars, laying an egg on the first caterpillar at the time she places it in the burrow. Further caterpillars are added and the burrow sealed permanently before the egg hatches. The mother then has no further contact with her offspring and starts on her next burrow: burrows are provisioned one at a time (e.g., Field, 1989). Other *Ammophila* species, however, are simultaneous progressive provisioners (SPP). In these, a mother digs a burrow, adds the first caterpillar, and lays an egg. She then closes the burrow temporarily and adds further caterpillars only once the egg has hatched and her larva has almost eaten the first caterpillar. While she waits for this to happen, the mother starts off another burrow and usually has two to four separate burrows in mid-provisioning at any one time (Baerends, 1941a,b; Field and Brace, 2004; Hager and Kurczewski, 1986; Weaving, 1989).

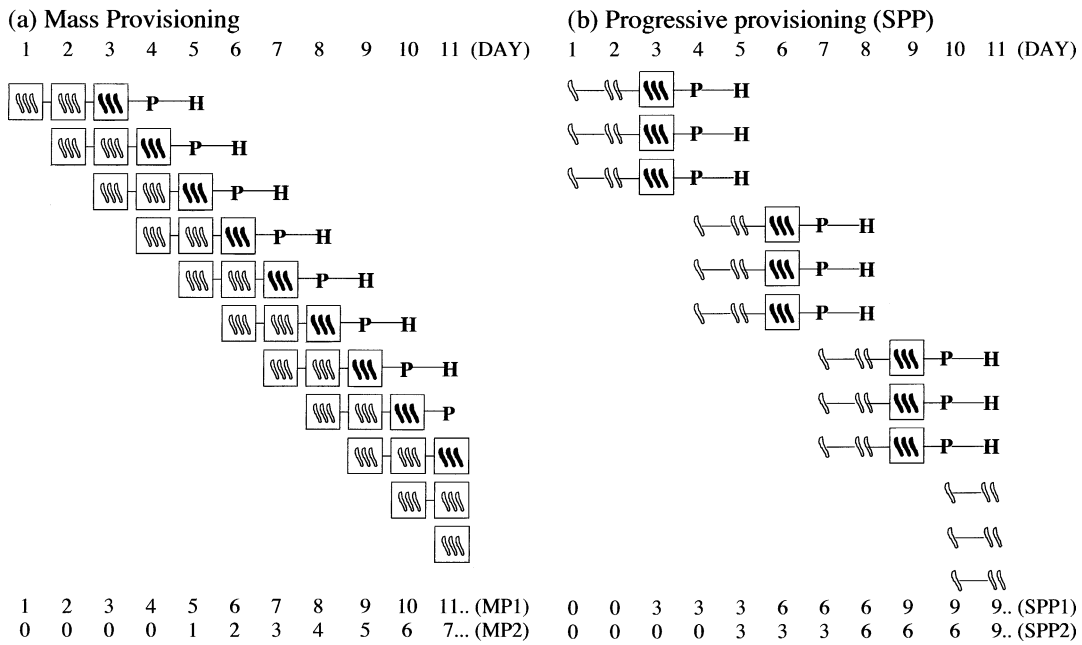
In order to visualize offspring production in this situation, consider a strategy in which mothers nest independently and mass provision one offspring at a time (MP). Each egg is laid

**Table 1**  
Parameters used in the simulations

Parameter	Meaning
$c$	Number of time periods a mother requires to collect the equivalent of a full provision mass, when conditions are suitable for provisioning
$\mu_{\text{Sun}}$	Mortality rate of mothers per time period that is suitable for provisioning
$\mu_{\text{Rain}}$	Mortality rate of mothers per time period that is unsuitable for provisioning
$broodsize$	Number of offspring provisioned simultaneously by a progressive provisioner in each batch
$p$	Probability that a time period will be unsuitable for provisioning
$h$	Probability that a fully provisioned offspring will mature if its mother dies
$t_{\text{larva}}$	Minimum larval development duration: the number of time periods a larva requires to become a pupa, assuming it is fully provisioned within that time
$t_{\text{pupa}}$	Pupal duration: number of time periods required for a fully fed offspring to mature into an adult once larval development is complete
avMPRS	The mean reproductive success of mothers using mass provisioning
avPPRS	The mean reproductive success of mothers using progressive provisioning

at the time of first provisioning, and each offspring is provisioned until it has received a fixed total amount of food, at which point the mother starts on the next offspring (Figure 1). When a mother dies, we assume that any offspring she has fully provisioned will mature normally and suffer no disadvantage through her absence, but that any offspring she has only part-provisioned will starve. The latter is an extreme assumption, but it is likely that mothers will at least obtain a lower rate of offspring fitness through partially provisioned offspring, and that below some minimum provision mass, part-provisioned offspring indeed starve. The SPP strategy is to collect provisions at the same rate as MP but to each day divide them equally among the offspring in a brood of size *broodsize* (see Figure 1). Thus, for example, if MP fully provisions one offspring per unit time and SPP provisions successive broods of three offspring, SPP completes no offspring in the first two time periods but completes her first brood of three offspring by the end of the third period by which time MP has also completed three offspring (Figure 1). This framework allows us to assume that MP and SPP suffer the same adult mortality rates: they have the same long-term oviposition rates, and they also collect provisions at the same rates—*foraging* is believed to be one of the costliest activities performed by adult wasps and bees (e.g., Cant and Field, 2001; Schmid-Hempel and Wolf, 1988; Strohm and Marliani, 2002).

In order to calculate cumulative reproductive success under MP and SPP, simulations analogous to Figure 1 were run assuming a constant adult mortality rate per time unit ( $\mu$ ). During each time step, the following five operations were performed. (1) First, a proportion of mothers died equal to  $\mu$  (proportion alive at start of the time unit), with the proportion alive set at 1.0 at the start of the simulation. (2) Mothers that died were assigned a final reproductive success equal to the cumulative number of offspring fully provisioned by the end of the previous time unit under the appropriate strategy (MP or SPP: see example in Figure 1). (3) The



**Figure 1**  
 A model of how reproductive success is accrued during (a) mass provisioning and (b) simultaneous progressive provisioning of batches of three offspring at a time (*broodsize* = 3). Each row of symbols represents a different offspring. In this example, an offspring requires three feeds to become fully provisioned, a mother can collect three feeds per day (*c* = 1), and offspring spend 3 days as larvae and 2 days as pupae before maturing as adults (*t<sub>larva</sub>* = 3, *t<sub>pupa</sub>* = 2). The rows labeled MP1 and MP2 give the cumulative reproductive success accrued by a mass provisioner that is still alive at the end of each day under Model 1 and Model 2, respectively. SPP1 and SPP2 give the equivalent figures for a progressive provisioner. [Single wavy line] Denotes an offspring that has received a single feed, [Two wavy lines] denotes an offspring that has received two feeds, [Three wavy lines] denotes a fully provisioned offspring, [Three wavy lines in a box] denotes a fully provisioned offspring that has finished feeding, P denotes a pupa, and H denotes a pupa that hatches to adulthood at the end of that day.

cumulative reproductive success of surviving mothers was then incremented according to the provisioning strategy concerned (e.g., MP1 and SPP1 in Figure 1). Simulations continued until less than 1% of mothers remained alive. At this point (4) the average reproductive success of the two strategies was calculated (the mean reproductive success of mothers using mass provisioning [avMPRS], the mean reproductive success of mothers using progressive provisioning [avPPRS]), with still-living mothers being assigned the cumulative number of offspring fully provisioned by the end of the final time unit. (5) The relative success of the two strategies was calculated as (avMPRS - avPPRS)/avMPRS. A negative value indicates an advantage to SPP; a positive value favors MP. Wasps and bees cannot forage in heavy rain or when it is too cold. In some simulations, I therefore included a constant probability *p* that a time unit would be unsuitable for foraging, determined independently for each time unit using a random number generator. Adult mortality could still occur on such days, but no provisioning took place, so that cumulative reproductive success did not increase. The effect of varying four parameters was examined (Table 1):  $\mu$ , *p*, *broodsize*, and *c*. Parameter *c* might reflect the abundance of provisions in the environment.

**Model 2: offspring become independent only when they reach adulthood**

Model 2 differs from Model 1 in the point at which a mother’s investment is converted into independent offspring. In Model 2, offspring become independent of their mothers only when they reach adulthood, not as soon as they are fully provisioned. Unlike the scattered, well-hidden nests of amorphilines, the majority of wasps and bees build nests containing

many offspring, each in a separate cell. Nest entrances are usually left open during foraging or after a mother’s death, and unguarded nests may be raided by generalist predators such as ants, which carry off offspring of all developmental stages. Simply through their continued presence, mothers may provide a degree of protection for their offspring even after provisioning is complete: death or experimental removal of mothers decreases the chance that adult offspring will emerge from the nest (e.g., Eickwort et al., 1996; Kukuk et al., 1998). The most vulnerable nests are probably the flimsy paper combs of open cells produced by many independent founding eusocial vespid wasps, which hang exposed on plants, rocks, and other substrata. Death of a lone foundress or all the adults on a multifemale nest often results in the death of most or all immature offspring, although some may be adopted by foreign conspecifics (e.g., Field et al., 1998, 2000; Nonacs and Reeve, 1993; Shreeves et al., 2003). Model 2 focuses on independent-nesting mothers with such exposed, multicellular nests.

In Model 2, adult mortality and provisioning occur as in Model 1, but a mother’s reproductive success is measured as the total number of offspring that reach adulthood before she dies, rather than the number that she has fully provisioned (Figure 1). Offspring that are fully provisioned but have not yet reached adulthood are assumed to fail if their mother dies, whereas in Model 1 such offspring were counted as “safe.” In order to simulate reproduction in this situation, it is necessary to specify how larval development is affected by the provisioning strategy using two new parameters, *t<sub>larva</sub>* and *t<sub>pupa</sub>* (Table 1). I assume that there is a minimum larval development duration (*t<sub>larva</sub>*) required for a larva to consume its food and grow, after which it becomes a pupa. A larva achieves the minimum development duration so long as it is fully provisioned within that time. If not,

the larva becomes a pupa only once it has been fully provisioned, and its actual development duration then exceeds the minimum duration. For example, if an MP mother requires one time period to fully provision each offspring ( $c = 1$ ) and  $t_{\text{larva}}$  is three time periods, each offspring is assumed to finish growing at the end of its third time period, even though it is fully provisioned by the end of its first period. It is a pupa at the start of its fourth period. With the same minimum larval duration, an SPP mother that provisions broods of five offspring simultaneously will finish provisioning each brood only at the end of their fifth time period. Her offspring therefore become pupae at the start of their sixth time period. I assume a constant pupal duration ( $t_{\text{pupa}}$ ), which is the same for all MP and SPP offspring.

In Model 2, pupae and fully provisioned larvae are assumed to continue development normally during periods that are unsuitable for provisioning. In contrast, partially provisioned larvae must wait until conditions become suitable again to become fully provisioned. For example, with  $t_{\text{larva}} = 3$ , if an MP mother fully provisions an offspring in time period 1 but the next two time periods are unsuitable for provisioning, her larva still becomes a pupa at the start of period 4. In contrast, an SPP offspring that receives only part of a full provision mass in period 1 is still a larva at the start of period 4 and becomes a pupa only once it receives the remainder of its provisions. Conditions during which fully provisioned immatures can develop but adults cannot forage may include rainy days and perhaps days that are too cool for adult flight but warm enough for immature development to continue.

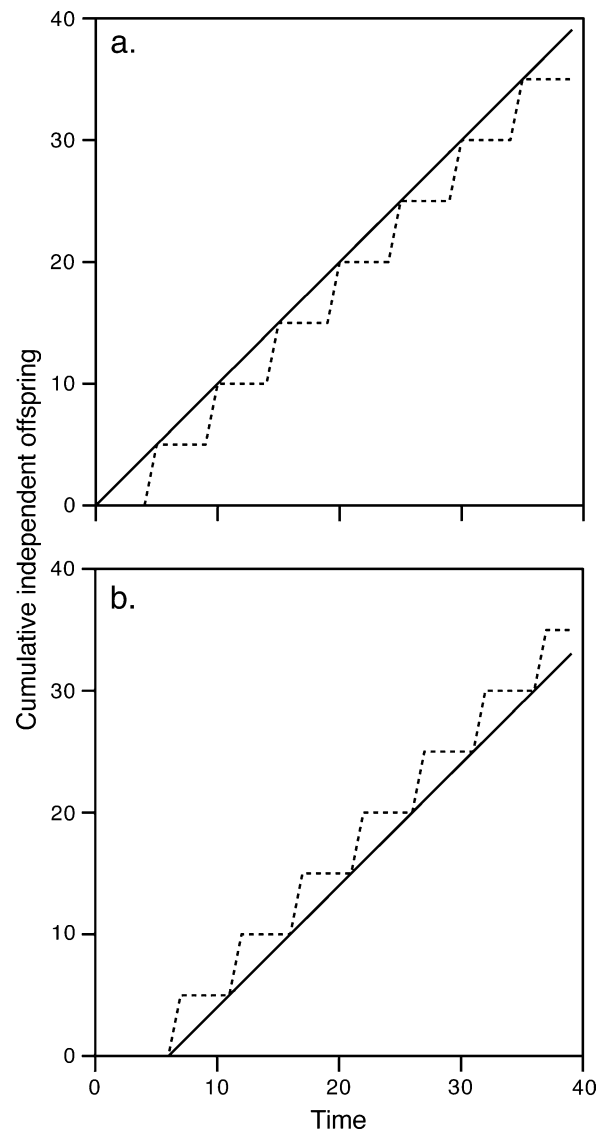
#### Intermediate models: fully provisioned offspring have an intermediate probability of maturing after their mother's death

Models 1 and 2 are at opposite extremes in terms of the chance that a fully provisioned offspring survives the death of its adult carer(s). Many taxa are probably intermediate in this respect. For example, Kukuk et al. (1998) found that experimental removal of adults from nests of a communally nesting halictine bee did not lead to total failure of offspring that had already been fully provisioned, but caused a 50% decrease in the number that matured, probably due to ant predation at undefended nests. In a nonsocial population of another halictine, the proportion of failed offspring increased from 15% with the mother present to 44% if she had died (Eickwort et al., 1996; see also Field, 1996; von der Heide, 1992). I therefore carried out further simulations in which the proportion of fully provisioned offspring that reach maturity after their mother dies ( $h$ ) was allowed to vary between 0 and 1.0.

## RESULTS

### Model 1

With no adult mortality ( $\mu = 0$ ), SPP has the same long-term offspring production rate as MP (Figure 2a). But once adult mortality is allowed (Figures 3 and 4), MP's lifetime productivity is greater, even though both strategies invest in offspring (e.g., forage) at the same rate. This is because when an SPP mother dies, more of her past investment is represented by incompletely provisioned offspring, which starve (Figures 1 and 2a). In Figure 1, for example, an SPP mother that dies at the end of day 2 has produced zero independent offspring, whereas an MP mother has produced two. The disadvantage that SPP suffers increases with increasing brood size: larger broods of offspring take longer to provision, so that the mother is more likely to die before she finishes. SPP is

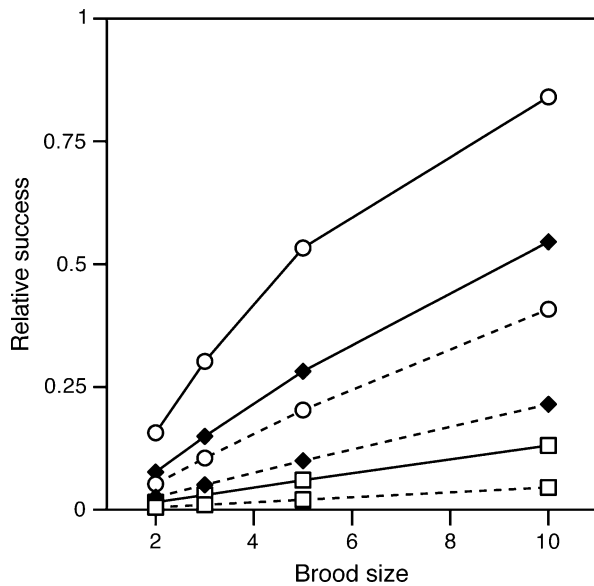


**Figure 2** Cumulative reproductive success over time with no adult mortality ( $\mu = 0$ ) and  $c = 1$  under mass provisioning (solid line) and under progressive provisioning with  $broodsize = 5$  (dashed line). (a) Model 1, (b) Model 2:  $t_{\text{larva}} = 3$  days,  $t_{\text{pupa}} = 2$  days.

least disadvantageous when  $broodsize = 2$  (Figure 3). SPP also becomes more disadvantageous as  $\mu$  increases (Figure 3). This is because SPP is the strategy that delays converting its investment into independent offspring for longest (Figure 1), so that its reproductive success is most affected by an increase in the adult mortality rate. For the same reason, if provisions become scarcer in the environment (increased  $c$ ), or if conditions are unsuitable for provisioning on some days but there is still adult mortality on those days, SPP does even worse relative to MP (Figures 3 and 4). In both these situations, mothers are effectively exposed to greater mortality per unit of food that they collect.

### Model 2

In Model 2, offspring become independent only when they reach adulthood, rather than at the end of provisioning. The most successful strategy is therefore the one that brings the maximum number of offspring through to adulthood before

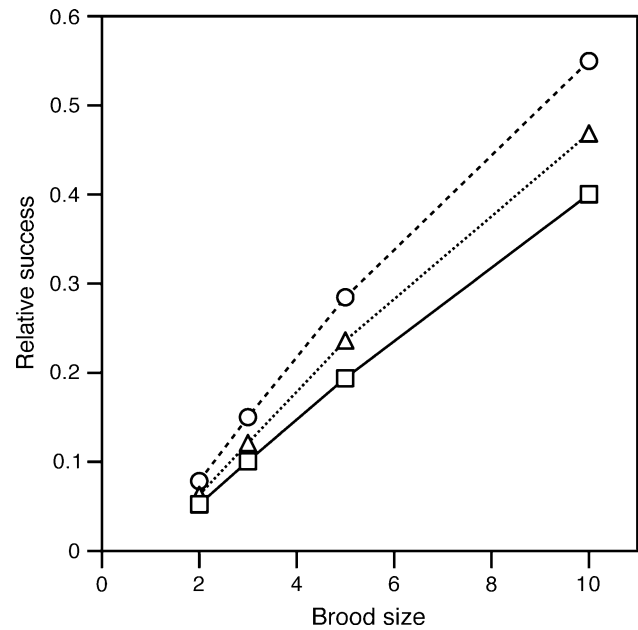


**Figure 3**

Model 1: effect of a progressive provisioner's brood size on the relative success of mass provisioning versus simultaneous progressive provisioning. Relative success is calculated as  $(avMPRS - avPPRS) / avMPRS$  (see text): positive values favor mass provisioning, negative values favor progressive provisioning. Results are shown for three different adult daily mortality rates ( $\mu$ ): 0.01 (squares), 0.05 (diamonds), and 0.1 (circles); and for  $c = 1$  (dashed lines) and  $c = 3$  (solid lines).  $p = 0$  in all cases.

the mother dies. SPP now has a demographic advantage over MP, so long as brood size is below a threshold value (Figure 5; see also Figure 2b). In Model 2, MP fully provisions each offspring more quickly than is necessary to minimize offspring development time (assuming  $t_{larva} > c$ ). By provisioning individual offspring more gradually, SPP can feed several offspring simultaneously without necessarily increasing their development times. Investment is converted into independent offspring more quickly than under MP, which initiates only one offspring at a time (Figure 1). SPP's reproductive success is maximized when brood size is as large as possible without causing actual larval development time to exceed the minimum set by  $t_{larva}$ . This optimum brood size is equal to  $t_{larva}/c$ , that is, the number of offspring that can be fully provisioned within the minimum larval development time (a brood size of 4 in Figure 5). Longer minimum larval development times or a greater abundance of provisions in the environment will therefore lead to an increase in the optimum brood size (Figure 6). With increasing brood size above the optimum, actual development duration begins to exceed the minimum as more larvae are provisioned simultaneously, until a threshold brood size is reached (approximately 7 in Figure 5) at which the increased developmental duration for SPP larvae cancels out the advantage of simultaneous provisioning.

Increasing the adult mortality rate in Model 2 further increases the advantage to whichever is the more successful strategy (Figure 5). As in Model 1, this is because the more successful strategy is the one that converts its investment into independent offspring with the least delay: below the threshold number of offspring provisioned simultaneously this is SPP, whereas above the threshold it is MP. Increasing the proportion of time periods that are unsuitable for provisioning has two effects. First, if adult mortality is allowed on unsuitable days, this has the same qualitative effect as increasing adult mortality on suitable days (as in Figure 5).



**Figure 4**

Model 1: effect of the proportion of days unsuitable for provisioning ( $p$ ) on the relative success of mass provisioning versus simultaneous progressive provisioning:  $p = 0$  (squares), 0.3 (triangles), and 0.5 (circles). Other parameter values:  $\mu_{sum} = 0.05$ ,  $\mu_{rain} = 0.025$ ,  $c = 1$ . Each point is the average from 200 runs of the simulation.

Second, on average a larger proportion of MP than SPP larvae are fully provisioned and can therefore continue developing on unsuitable days, favoring MP. The overall effect of adding unsuitable days to the simulation is shown in Figure 7. With a large proportion of unsuitable days, the "development" effect can favor minimizing the brood size under SPP, as in Model 1 (Figure 7, top line).

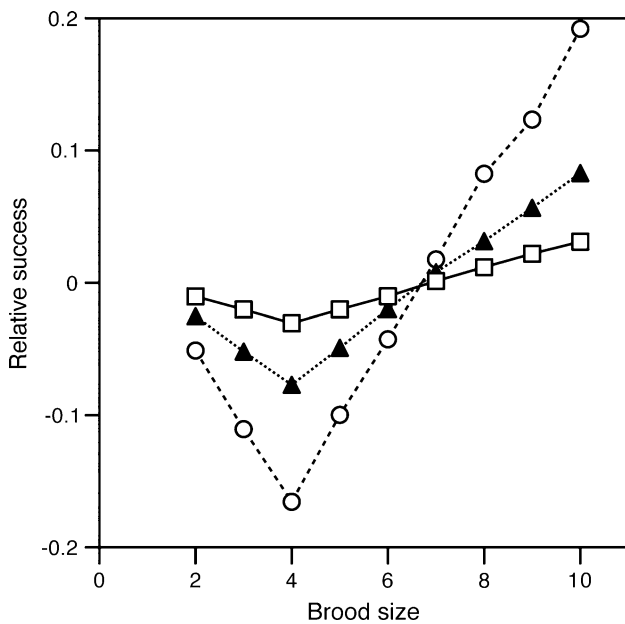
### Intermediate models

Figure 8 shows the effect of varying the proportion of fully provisioned offspring that reach maturity after their mother dies ( $h$ ) in Model 2. Whenever a mother dies, her reproductive success is now calculated as the number of her offspring that have already reached adulthood plus the product of  $h$  and the number of fully provisioned but immature offspring. As  $h$  increases, the advantage to SPP decreases. The relationship between fitness and the number of offspring provisioned simultaneously under SPP becomes less strongly "V" shaped, until the optimum brood size becomes 1, as in Model 1. These results suggest that the potential advantage to SPP will be outweighed by the disadvantage of prolonged dependency if fully provisioned offspring have more than a small or moderate chance of surviving their mother's death. It is then the number of offspring that a mother has fully provisioned before her death that primarily determines her reproductive success, rather than the number that have reached adulthood, and progressive provisioning prolongs the provisioning period.

## DISCUSSION

### Evolution of progressive provisioning in Model 1

An important conclusion from Model 1, where offspring become independent at the end of provisioning, is that the average mother always produces fewer offspring under

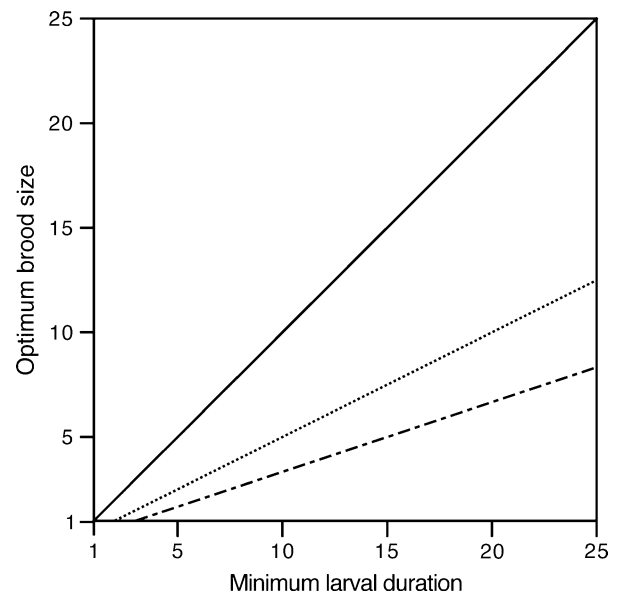


**Figure 5**  
Model 2: effect of a progressive provisioner's brood size on the relative success of mass provisioning versus simultaneous progressive provisioning: positive values favor mass provisioning, negative values favor progressive provisioning. Results are shown for  $c = 2$ ,  $p = 0$ ,  $t_{\text{larva}} = 8$  days,  $t_{\text{pupa}} = 15$  days, and for three different adult daily mortality rates ( $\mu$ ): 0.01 (squares), 0.025 (triangles), and 0.05 (circles).

simultaneous progressive provisioning than under mass provisioning (Figures 3 and 4). For simultaneous progressive provisioning to evolve in the face of this disadvantage, the offspring produced must be of higher quality than mass provisioned offspring or fewer resources must be wasted on offspring that fail. I first discuss evidence that progressive provisioning can lead to fewer resources being wasted, and calculate in ammophilines whether this is a large enough advantage to outweigh the disadvantage of prolonged dependency. I then discuss other predictions from Model 1 that could be tested in future work.

Field and Brace (2004) show that the extended parental care inherent in progressive provisioning can reduce the costs of immature mortality in two distinct ways. The first is a reduction in mortality from parasites that are introduced to offspring cells during provisioning events. Examples are the larvae of cuckoo parasites such as miltogrammine flies (Diptera). Adult flies follow prey-carrying mothers back to their nests and deposit maggots that destroy the wasp immature and then eat the provisions. Each provisioning event represents an opportunity for parasites, but under mass provisioning an offspring receives all of its feeds while still an egg, whereas under progressive provisioning only the first event occurs before the offspring is a larva. Field and Brace (2004) show that *Ammophila* larvae are much more likely to survive parasitism than eggs, so that progressive provisioning provides an advantage (see also Hager and Kurczewski, 1985). Other wasps that provision progressively lay each egg in an empty cell, adding no prey at all until just before or after the egg hatches (e.g., Evans, 1966). Such species may be immune to miltogrammine attack.

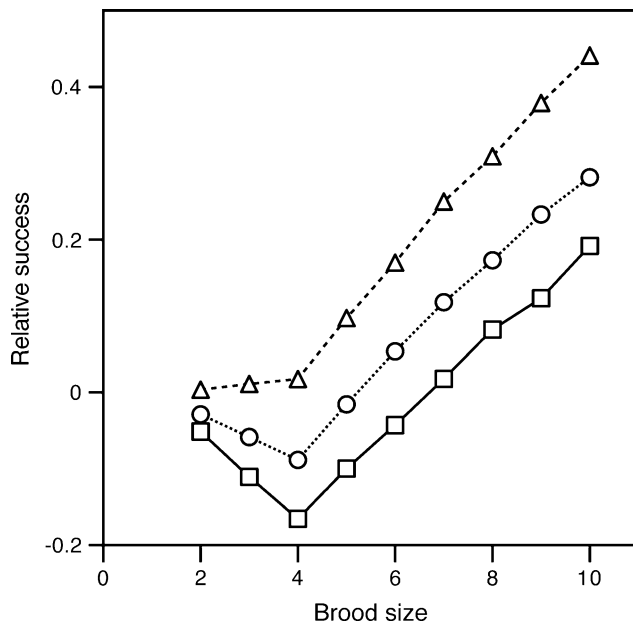
The second way in which progressive provisioning can reduce the costs of offspring failure is if mothers can intervene or terminate investment prematurely in failing offspring (Trumbo, 1996). Here, the key aspect of progressive provisioning is that a mother continues to visit her offspring as it



**Figure 6**  
Model 2: effect of minimum larval development duration ( $t_{\text{larva}}$ ) on the optimum brood size, with  $c = 1$  (solid line),  $c = 2$  (dotted line),  $c = 3$  (dot-dash).

grows, but before she has invested fully in it. She is therefore in a position to detect mortality factors that become apparent only gradually and avoid wasting a full quota of investment on affected offspring. Relevant mortality factors include failure of eggs to hatch, larval diseases, provisions going moldy due to fungal attack, and cuckoo parasites that become more detectable as they destroy the host immature and grow larger feeding on the provisions (Field and Brace, 2004). Field and Brace (2004) show that in *Ammophila*, progressively provisioning mothers terminate investment in cuckoo-parasitized offspring. In contrast, because she fully provisions her offspring before her egg even hatches, termination of investment is not an option for a mass provisioning mother, even if she subsequently discovers that her offspring is failing.

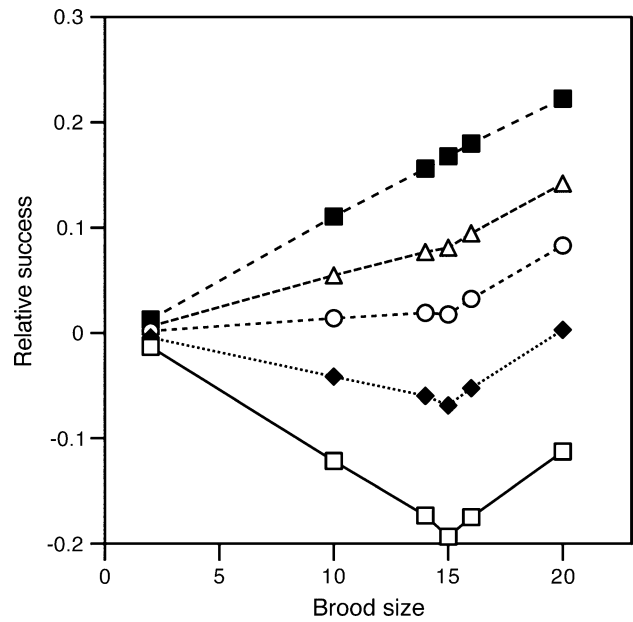
The Model 1 simulation can be used to predict how much of a mass provisioner's investment needs to be wasted through immature mortality that is avoided under simultaneous progressive provisioning, in order to balance the disadvantage to a progressive provisioner of starvation among offspring that she has provisioned only partially when she dies. The extra avoidable mortality required, expressed as a proportion of a mass provisioner's investment, is shown as the y-axis in Figures 3 and 4. Adult mortality rates are not available for ammophiline females. But if  $\text{broodsize} = 2$ ,  $c = 1$ , and  $\mu$  is between 0.01 and 0.1 as in other wasps, 0.5–5% of the investment of mass provisioning mothers must be wasted through mortality factors avoided under simultaneous progressive provisioning (Figure 3). Adding a probability of 0.2–0.5 that days are unsuitable for provisioning, with  $\mu = 0.025$ –0.05, the avoidable mortality required would be 3–5% (Figure 4). Among six MP *Ammophila* populations that can utilize more than one prey per offspring, an average of 4.7% of offspring are destroyed by miltogrammine fly maggots (standard error 0.02%, range 0–13%: Field, unpublished data). This is broadly consistent with the mixed occurrence of progressive provisioning and mass provisioning among ammophilines (5 progressive provisioners out of 13 species that can utilize more than one prey per offspring: Field, unpublished data).



**Figure 7**  
Model 2: effect of the proportion of days unsuitable for provisioning ( $p$ ) on the relative success of mass provisioning versus simultaneous progressive provisioning:  $p = 0$  (squares), 0.25 (circles), 0.5 (triangles). Other parameter values:  $\mu_{\text{Sun}} = 0.05$ ,  $\mu_{\text{Rain}} = 0.025$ ,  $t_{\text{larva}} = 8$  days,  $t_{\text{pupa}} = 15$  days,  $c = 2$ . Each point is the average from 200 runs of the simulation.

The mode of progressive provisioning in ammophilines is also consistent with its primary function being to reduce the costs of interspecific parasitism. Mothers wait until the egg hatches before adding the second prey item but then add multiple prey without waiting for each to be eaten (Baerends, 1941a,b; Hager and Kurczewski, 1986; Field, Shreeves G, and Brace S, unpublished data). Parasite larvae are probably detected only once they have destroyed the wasp egg and grown larger: by minimizing investment before egg hatch, mothers minimize the potential costs of investment termination. Once they have hatched from the egg, however, immatures are much less vulnerable to parasites (Field and Brace, 2004): further provisioning events no longer represent significant exposure and so need not be delayed.

The extent to which offspring mortality can be avoided under progressive provisioning depends on the kind of mortality factors that operate. For example, progressive provisioning may lead to reduced costs of attack by cuckoo parasites but might provide no advantage against parasitoids, which typically begin feeding on wasp immatures only after they are full grown. Also, progressive provisioning may initially provide an advantage through reducing the costs of parasitism, but if the parasites concerned are thus forced to extinction, this advantage could not subsequently maintain the progressive provisioning strategy. Whether parasites go extinct after the evolution of host defenses may depend on whether they have alternative hosts. Miltogrammine flies appear to be extreme generalists, with some species recorded attacking more than 15 different host genera (e.g., Evans, 1966; Spofford and Kurczewski, 1990). Reduction of the costs of parasitism by miltogrammines may thus be important in both the origin and continued maintenance of progressive provisioning in ammophilines. In contrast, while it is possible that progressive provisioning by polistine wasps initially provided an advantage against cuckoo parasites, polistines today are attacked primarily by parasitoids (Yamane, 1996).



**Figure 8**  
Effect of varying the chance that a fully provisioned offspring survives the death of its mother ( $h$ ) on the relative success of mass provisioning versus simultaneous progressive provisioning:  $h = 0$  (open squares), 0.2 (diamonds), 0.4 (circles), 0.6 (triangles), 1.0 (filled squares). Other parameter values:  $p = 0$ ,  $\mu_{\text{Sun}} = 0.025$ ,  $t_{\text{larva}} = 15$  days,  $t_{\text{pupa}} = 15$  days,  $c = 1$ .

Model 1 predicts that if progressive provisioning does evolve in taxa where offspring become independent once they are fully provisioned, the number of offspring provisioned simultaneously should be minimized (Figure 3): it takes longer to finish provisioning a larger batch of offspring, so that the mother is more likely to die before her investment is converted into independent offspring. Field data from progressively provisioning ammophilines support this prediction: only two to four offspring are provisioned at once (Baerends, 1941a; Weaving, 1989; Field, Shreeves G, and Brace S, unpublished data). Furthermore, mothers may to some extent focus investment on a particular offspring until completion, only then adding prey to other offspring that they have previously provisioned minimally (Baerends, 1941a,b; Field, Shreeves G, and Brace S, unpublished data). Offspring may therefore be provisioned somewhat sequentially, reducing the disadvantage of simultaneous progressive provisioning compared with the simulation, where it is effectively assumed that feeds are given in turn to the different offspring in a brood (Figure 1). Model 1 also predicts that the occurrence of progressive provisioning will correlate with low maternal mortality rates, high abundance of provisions in the environment, low frequencies of days that are unsuitable for provisioning, and high levels of offspring mortality that can be ameliorated through progressive provisioning (Figures 3 and 4). Data to test these predictions are currently unavailable, but ammophilines include several independent origins of progressive provisioning and represent excellent material for future comparative tests.

#### Evolution of progressive provisioning in Model 2

Contrary to the predictions of Model 1, eusocial vespid wasps are progressive provisioners but do not appear to minimize brood size. Even lone foundresses, whose offspring depend entirely on their mother's survival, often provision broods of 10–30 offspring at once (e.g., Mead et al., 1994; Reeve, 1991;

Spradbery, 1973). In this context, an important difference between eusocial vespids and ammophilines is that vespid nests are much more exposed, so that even fully provisioned offspring have only a small chance of surviving predation if their mother dies (e.g., Field et al., 1998, 2000). Vespid offspring thus become independent of their mothers only at adulthood, instead of at the end of provisioning. When offspring reach independence only at adulthood, Model 2 shows how simultaneous progressive provisioning can provide a demographic advantage over mass provisioning. A progressive provisioner initiates the development of several offspring at once. So long as brood size does not exceed a threshold value, these offspring reach adulthood earlier on average than the offspring initiated sequentially by a mass provisioner (Figures 1 and 5). Note that this demographic advantage is in addition to any advantage through reducing the costs of immature mortality that progressive provisioning may provide (Field and Brace, 2004). This two-fold advantage suggests that simultaneous progressive provisioning should evolve most easily in species with exposed nests.

Under Model 2, mothers are no longer expected to minimize brood size. The optimum brood size is positively correlated with minimum larval development time and the abundance of provisions in the environment. This leads to the prediction that, all else being equal, there should be a positive correlation between these two factors and brood size among progressive provisioners (Figure 6). There are currently insufficient data available to test this prediction, but there is considerable variation in the actual duration of larval development among vespid wasps, from 10–15 days in many polistines to 60 days in the stenogastrine *Liostenogaster flavolineata* (Mead et al., 1994; Nonacs and Reeve, 1993; Samuel, 1987).

In Model 2, a long period of offspring dependency is assumed already present. simultaneous progressive provisioning then need not prolong further the period of dependency compared with mass provisioning; a larva fed progressively may reach adulthood just as fast as if it received its entire food store at the start of development. Progressive provisioning prolongs dependency only if brood size increases to the point where offspring development as a whole is lengthened (Figure 5).

### Intermediate models

In Model 1, fully provisioned but immature offspring are assumed to always survive their mother's death, whereas in Model 2 they never survive it. Burrowing wasps and bees with multicellular nests are probably intermediate in this respect (Eickwort et al., 1996; Kukuk et al., 1998; Michener, 2000). As the chance of immatures surviving their mother's death ( $h$ ) increases, the dependent period starts to correspond more and more closely to the period of provisioning, and the potential advantage provided by progressive provisioning is offset because progressive provisioning effectively prolongs offspring dependency. When  $h$  is above a threshold value, mass provisioning becomes the better strategy unless additional advantages, such as those suggested by Field and Brace (2004), operate to favor progressive provisioning (Figure 8). These results lead to the prediction that across taxa, the occurrence of progressive provisioning should be negatively correlated with the probability that fully provisioned offspring survive their mother's death.

### Further refining the models

The models could easily be refined to take more specific life-history data into account. For example, there are no

published data on how larval development is affected by variation in the provisioning rate or on the possibility that larvae starve if poor conditions prevent provisioning for long enough. I have also assumed that partially provisioned offspring fail completely, whereas it is possible that above a threshold provision mass, they mature successfully to produce adults of suboptimal size. Finally, I have for simplicity assumed that progressively provisioning mothers divide daily provisions equally between the offspring in their current brood. Provisions themselves may not always be completely divisible (e.g., *Ammophila*), and another strategy would be to feed the offspring within a brood at different rates, so that their development is staggered. Although the main trends I have outlined should remain the same, such refinements would allow more precise predictions to be generated for particular taxa.

### Progressive provisioning and the evolution of helping

A long period of offspring dependency provides potential helpers with a large insurance-based advantage over independent-nesting females (Gadagkar, 1990; Queller, 1994, 1996; Reeve, 1991). My analysis suggests two ways in which a long dependency could arise in an ancestral nonsocial species. First, starting with a well-hidden nest of the kind built by many ground-nesting wasps and bees, the evolution of progressive provisioning would prolong the dependent period (Model 1). Field and Brace (2004) show how progressive provisioning can reduce the costs of immature mortality. Progressive provisioning could evolve if this benefit is large enough to outweigh the cost of any resulting increase in offspring dependency. Model 1 in combination with the data from ammophiline wasps discussed above suggests that this scenario is not unrealistic: the required reduction in the costs of immature mortality need not be unreasonably large even in nonsocial species. It will generally, however, need to be even smaller in species that are already eusocial: the death of a female living in a group does not necessarily lead to the death of all the offspring she has only partially reared, so that a longer dependency is less costly (Field et al., 2000; Shreeves et al., 2003).

Under the previous scenario, the large brood sizes seen in today's primitively eusocial wasps would result from the evolution of exposed nests after helping itself had evolved (Model 2). A second possibility is that exposed nests of the kind found in *Polistes* evolved before eusociality. There would then be a long period of dependency and large insurance-based advantages to potential helpers, but this would be independent of the provisioning strategy. This second scenario, however, leaves unanswered the question of why exposed nests themselves evolved if they led to an increase in offspring dependency. The order in which simultaneous progressive provisioning, helping, and exposed nests evolved in the ancestors of eusocial taxa such as vespids is currently unknown and will require phylogenetic work in combination with studies of the natural history of nonsocial sister groups (e.g., Schwarz et al., 2003).

### Conclusion

The analysis above suggests two sets of ecological conditions under which simultaneous progressive provisioning might evolve. The first is when fully provisioned offspring have only a small chance of maturing after the death of their mother. Reproductive success then depends on bringing offspring through to adulthood rather than on just completing provisioning, giving simultaneous progressive provisioning a potential demographic advantage over mass provisioning



(Figure 2b). The chance that offspring can mature after the death of their mother will depend on habitat, nest type and other natural history details. The second situation in which simultaneous progressive provisioning might evolve is where there is enough offspring mortality suffered under mass provisioning that can be avoided through the extended parental care that is inherent under progressive provisioning (Field and Brace, 2004). At one extreme, ammophiline wasps probably benefit only through the second mechanism, whereas eusocial vespids benefit primarily through the first. Ground-nesting wasps and bees with multicellular nests, such as halictines, may be intermediate.

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