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# When nesting involves two sequential, mutually exclusive activities: what's a mother to do?

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## ABSTRACT

**Background:** Parents can invest in offspring through a variety of behaviours, some of which trade off against each other, such as investment in the current brood versus investment in a future one.

**Question:** When should hymenopteran parents stop provisioning the current nest and decide whether to seal the entrance to the nest (e.g. with a number of leaf pieces)?

**Method and key assumptions:** A dynamic state variable model. We assume that mothers alter reproductive decisions based on their perception of costs and benefits of brood cell and nest construction. Some of these construction behaviours allocate investment at one or a few offspring in a brood but others affect the entire brood.

**Conclusions:** Several factors impact the decisions of when to cease provisioning new offspring and whether to seal the nest. Higher current nest value and greater risk of mortality increase the likelihood of both ceasing provisioning earlier and sealing the nest. The greater the benefit of sealing, either because of increased benefits or decreased negative impacts, the earlier and the more frequently it occurs.

*Keywords*: dynamic state variable model, Hymenoptera, nest provisioning decisions, offspring sex ratio, resource allocation, solitary bee.

## INTRODUCTION

A central life-history decision is when to terminate investment in the current reproductive event. The basic assumptions used in analysing this decision are that the benefit to the parent(s) from the current brood increases with continued investment (though with diminishing returns), while at the same time the opportunity or capacity for future reproduction is reduced (Williams, 1966a, 1966b). Investment is predicted to be terminated when the benefit (measured as the marginal fitness gain from the current brood) and cost (measured as the marginal fitness loss due to foregone future reproduction) of further investment are equal.

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This 'present–future trade-off' is conceptually simple because it idealizes investment as a single, continuous variable. In nature, however, parents invest in offspring with a variety of behaviours that serve different purposes. Parents may bring several types of food, build nests, defend the young from predators, and keep the offspring warm. Some of these behaviours direct investment at one or a few offspring in a brood, whereas others affect the entire brood. Few studies, either theoretical or empirical, on the present versus future trade-off address this complexity (but see Rosenheim *et al.*, 1996).

Here we use a dynamic state variable model (Mangel and Clark, 1988; Clark and Mangel, 2000; e.g. Clark and Butler, 1999; Alonzo, 2002) to examine solitary bee decisions in which parents terminate one type of investment by ceasing behaviours of one type (provisioning) and engaging in another type of investment (sealing the nest). The value of sealing the nest is the result of better protection of the offspring in the nest from predators, parasites, and other dangers. We find that the differing nesting behaviours are easily incorporated into the above framework and considering them expands the range of interesting phenomena explained (e.g. gender order of offspring).

In solitary bees, mothers construct nests consisting of a number of brood cells, built and provisioned sequentially (Freeman, 1981). After a certain amount of provision has been accumulated in a cell, an egg is laid, the cell is closed, and work begins on the next cell. The adult size of offspring is strongly correlated to the amount of pollen (we refer to pollen and nectar collectively as simply pollen) that is provisioned to the brood cell (Klostermeyer *et al.*, 1973; Bosch and Vicens, 2002). All of the food consumed by the developing progeny prior to adulthood is provided by the mother. Furthermore, the haplo-diploid sex determination of hymenoptera allows the mother bee to control the sex of her offspring. After a certain number of cells are completed, the entire nest is sealed and a new nest initiated elsewhere. Sons and daughters are often differently-sized and accorded different amounts of provision (Klostermeyer and Gerber, 1969; Klostermeyer *et al.*, 1973; Alcock, 1979; Cowan, 1981). Sealing ('capping') of the nest entrance provides extra protection from enemies, mostly parasitoids, and therefore likely increases the value of those offspring now sealed in the nest. However, sealing prevents the mother from constructing more brood cells at that site, so that after sealing, time and energy must be spent to search for a new nest site for future offspring.

The alfalfa leafcutter bee, *Megachile rotundata*, was used as our model species and parameter values were either known or determined through experimental work reported elsewhere (Peterson, 2004, Peterson and Roitberg, 2006a, 2006b). In our fieldwork using this species, we observed that nests were often sealed early in the season before the nest cavity was completely full (J.H. Peterson and B.D. Roitberg, unpublished data). We also found that the size of the sealing 'cap' and even the number of 'caps' in a nest varied among individual females (Peterson, 2004). This suggests that the conditions experienced by a mother impact how much is invested to seal the nest (i.e. the size of the 'cap').

Risk of adult mortality likely impacts the trade-off between making one large nest or several small nests. The trade-off between many small nests versus a few big nests is complicated by sealing in that it gives a single incremental change in current nest value and at the same time decreases the chance of initiating new nests via time and mortality costs.

According to Clark's (1994) asset protection principle, the more valuable the nest, the more risk-averse the mother is predicted to become. In the real world, protecting all brood cells via sealing is important because if any brood cell becomes parasitized, parasitoid offspring (e.g. *Pteromalus* spp.) typically emerge as adults before the bees in the nest, allowing further brood cells to be parasitized.

In summary, we develop theory to elucidate the complex interactions between termination decisions, state dependence, and asset protection.

## METHODS

We use a dynamic state variable model to study investment termination behaviour in the solitary bees. Our model examines how much a bee is predicted to provision to each offspring, how many offspring to produce in a nest, the gender of the offspring, when to seal the nest, and how these decisions interact. We assume that the mechanisms underlying these decisions evolved to maximize expected lifetime reproductive success.

The state variables in our model (Table 1) are the amount of provision in the current brood cell ($P$ = pollen state) and the total value of completed brood cells (based on size, sex, and number) in the current nest ($V$ = nest state). Time is considered in discrete units ($t$). Within each time unit the female bee faces a fixed probability of death and the mother has a decision to make: (1) add more pollen to the current brood cell; (2) lay a male egg (son) and complete the brood cell; (3) lay a female egg (daughter) and complete the cell; or (4) seal the nest entrance and search for a new nesting site. The value of sealing the nest is determined by the nest state at the time of sealing.

A basic assumption in the model is the shape of the function relating the amount of pollen provisioned to each offspring to maternal fitness (Fig. 1). Here, fitness is defined as the number of copies of alleles passed on to future generations wherein parents who invest more in an offspring generally accrue greater fitness returns from that offspring.

**Table 1.** Summary of state variables and other parameters used in the dynamic state variable model, and forward simulation of offspring allocation decisions in solitary bees

| Variable or parameter | Description | Range of values tested |
|---|---|---|
| **Time** | | |
| $T$ | Total number of time units | 250 |
| $t$ | Time units | (1, 250) |
| **State variables** | | |
| $p(t)$ | Current pollen value collected | (0, 9) |
| $v(t)$ | Current nest value | (0, 49) |
| **Parameters** | | |
| $\mu$ | Chance of death per time unit | (0, 0.1) |
| $k$ | Multiplier of nest value from sealing | (1, 5) |
| $t_{\mathrm{p}}$ | Time required to add pollen | (0.5, 2) |
| $t_{\mathrm{m}}$ | Time required to produce a son | (1, 5) |
| $t_{\mathrm{f}}$ | Time required to produce a daughter | (1, 5) |
| $t_{\mathrm{s}}$ | Time required to seal the nest | (1, 30) |
| $t_{\mathrm{n}}$ | Time required to find new nest site | (1, 10) |
| $o_{\mathrm{m}f(p)}$ | Fitness benefit for producing a son (m) as a function of the amount of pollen in the brood cell ($p$) | Based on equation (1a) |
| $o_{\mathrm{f}f(p)}$ | Fitness benefit for producing a daughter (f) as a function of the amount of pollen in the brood cell ($p$) | Based on equation (1b) |

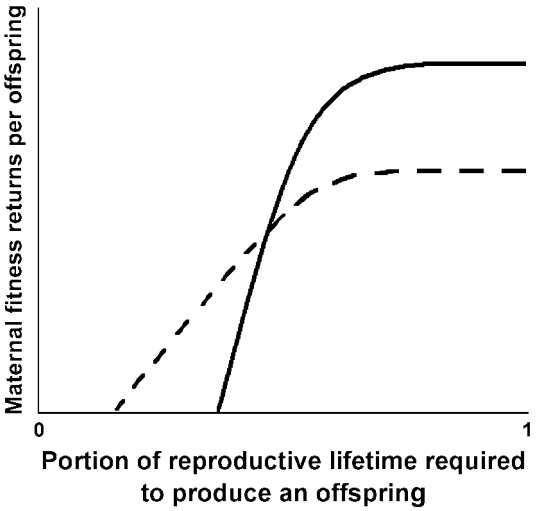


**Fig. 1.** Assumed maternal fitness gain as a function of the amount of time spent provisioning a single son (- - -) or daughter (—) for a given environment. Maternal fitness is considered the number of copies of alleles passed on to future generations wherein parents who invest more in an offspring generally accrue greater fitness returns from that offspring. [Easily obtainable resources would mean that both curves would reach the upper limit earlier (further to the left), whereas the opposite would occur if resources were more difficult to obtain.]

Our model is basically heuristic. However, where possible, real time values are used in an attempt to more closely represent reality. We make three basic assumptions in drawing the maternal fitness functions. First, there are diminishing returns, so that the mother's fitness gain from successive pollen deliveries (i.e. the marginal fitness) falls. Second, each daughter requires more initial investment (they are larger), but eventually gives higher fitness returns. Third, we have ignored potential population sex ratio effects on these functions (e.g. if males were rare, their value would be higher). Our individual-based tactical model does not take into account the decisions made by other females in the population (i.e. no frequency dependence). We assume that the sex ratio of the breeding population as a whole is stable and that the population is large and therefore the relative values of sons and daughters are not being altered by one sex becoming more rare. This assumption simplifies the analysis, and allows some insight to be gained into the problem (but it would clearly be unacceptable in an analysis of the sex ratio itself).

These assumptions in combination with previously proposed fitness curves for species such as *M. rotundata*, which have larger females than males (Frank, 1995; Rosenheim *et al.*, 1996), were used to develop our maternal fitness return curves:

$$f_{\mathrm{m}} = -4 + (a_{\mathrm{m}}\,(1 - \mathrm{e}^{-(p\gamma_{\mathrm{m}})})) \tag{1}$$

$$f_{\mathrm{f}} = -6 + (a_{\mathrm{f}}\,(1 - \mathrm{e}^{-(p\gamma_{\mathrm{f}})})) \tag{2}$$

where $f_{\mathrm{m}}$ is the fitness for a son (male) and $f_{\mathrm{f}}$ is the fitness for a daughter (female). The variables $a_{\mathrm{m}}$ and $a_{\mathrm{f}}$ control the asymptote of the curve of males (m) and females (f), respectively, and $\gamma$ controls the slope based on the number of pollen loads ($p$) and the sex.

This model produces two matrices: one stores optimal decisions (calculated by backward induction and used in a forward iteration for a simulated population of adult *M. rotundata* to derive predictions) and the other stores fitness values for those decisions for all combinations of state values; linear interpolation is used to calculate fractional fitness values (Mangel and Clark, 1988). The range of state variables is set large enough to allow sufficient resolution to see changes occur when conditions are altered (pollen values 0–9; nest values 0–49; time 1–250).

### *State dynamics*

There are two state variables, pollen state ($P$) and nest state ($V$), which can change each time state ($t$) depending on the decision made by the mother. The four possible decisions described earlier are: add pollen, produce a son and complete the brood cell, produce a daughter and complete the brood cell, or seal the nest. The state dynamics are (see Table 1 for an explanation of the terms):

If the decision is to add pollen,

$$P(t + t_{\mathrm{p}}) = P(t) + 1 \tag{3}$$

$$V(t + t_{\mathrm{p}}) = V(t) \tag{4}$$

where $t_{\mathrm{p}}$ is the time required to collect a load of pollen.

If the decision is to produce a son,

$$P(t + t_{\mathrm{m}}) = 0 \tag{5}$$

$$V(t + t_{\mathrm{m}}) = V(t) + o_{\mathrm{m}f(p)} \tag{6}$$

where $o_{\mathrm{m}f(p)}$ is the increment in nest value for adding a son of pollen value ($p$) and $t_{\mathrm{m}}$ is time required to deposit a male egg and close the brood cell.

If the decision is to produce a daughter,

$$P(t + t_{\mathrm{f}}) = 0 \tag{7}$$

$$V(t + t_{\mathrm{f}}) = V(t) + o_{\mathrm{f}f(p)} \tag{8}$$

where $o_{\mathrm{f}f(p)}$ is the increment in nest value for adding a daughter of pollen value ($p$) and $t_{\mathrm{f}}$ is the time required to deposit a female egg and close the brood cell.

If the decision is to seal the nest,

$$P(t + t_{\mathrm{s}}) = 0 \tag{9}$$

$$V(t + t_{\mathrm{s}}) = 0 \tag{10}$$

Once a nest is sealed, no further fitness can be gained from that nest and a new nest site must be found. Therefore, the $P$ and $V$ values are reset to 0.

### *Fitness increment*

Fitness is accrued in two ways, the production of an offspring (son or daughter) and sealing of the nest. This value of sealing the nest is calculated by multiplying the current value of the nest, $V(t)$, by the multiplier value for sealing the nest, $k$.

### *Terminal fitness*

All fitness is accrued through offspring production, provisioning, and sealing. Thus when $t = T$, $F(p, v, T) = 0$ for all values of $P$ and $V$.

### *Dynamic programming equation*

The dynamic programming equation (11) can be read as follows: Line 1, right-hand side, calculates the expected fitness from adding pollen discounted by survival while collecting pollen; Line 2, right-hand side, current plus expected fitness from producing a son ($f_{\mathrm{m}}$), discounted by survivorship ($1 - \mu$) during the son production process; Line 3, right-hand side, same as above but for a daughter ($f_{\mathrm{f}}$); and Line 4, right-hand side, fitness from sealing discounted by survival while sealing plus expected fitness discounted by survival while seeking a new nest. The maximum term refers to the decision to commit to one of the four mutually exclusive behaviours just described.

$$F(p,v,t) = \begin{bmatrix} (1-\mu)F(p+1,\, v,\, t+t_{\mathrm{p}}) \\ f_{\mathrm{m}} + (1-\mu)^{t_{\mathrm{m}}} F(0,\, v + o_{\mathrm{m}f(p)},\, t+t_{\mathrm{m}}) \\ f_{\mathrm{f}} + (1-\mu)^{t_{\mathrm{f}}} F(0,\, v + o_{\mathrm{f}f(p)},\, t+t_{\mathrm{f}}) \\ (1-\mu)^{t_{\mathrm{s}}} vk + (1-\mu)^{t_{\mathrm{n}}} F(0,\, 0,\, t+t_{\mathrm{s}}+t_{\mathrm{n}}) \end{bmatrix} \tag{11}$$

The basic parameter values are estimated when data are not available. A given value was chosen that would produce biologically meaningful results (e.g. reasonable number of offspring produced in a lifetime), making sensitivity analysis more informative.

We varied the time required to provision a brood cell, risk of adult mortality ($\mu$), value of sealing the nest ($k$), time required to locate a new nest site, and the shape of the maternal fitness return curves. The numerous mortality factors (e.g. predators and parasitoids) were generalized into a background mortality factor that assumes there is a given chance of death for every time unit, allowing the model to be more generally applicable.

There are no reliable data available on the value (fitness benefit) of sealing a nest ($k$) for solitary hymenopterans. Therefore, we considered a wide range of values from zero increase in nest value to a five-fold increase in the value of the nest.

## RESULTS

The decision matrix (i.e. the result of the backward induction) is shown for a specific time value in Fig. 2. The baseline values for the variables used in the model are: total time = 250, chance of death per time unit ($\mu$) = 0.02, time to collect pollen = 1, time to lay a female or male egg and close the broad cell = 3, time to seal the nest = 4, time to find a new nest site = 3, and multiplier for the value of the nest when sealed = 1.2.

When there is little pollen in the nest the mother will continue provisioning, as the marginal gain of further deliveries is high. If a cell is fully provisioned she will lay a female egg and close the cell. If the cell is partially provisioned she will lay a male egg and close the cell. As nest state increases, the mother is more likely to seal the nest. With regard to the impact of time, once $t < 200$ decisions are essentially stationary (97% congruence) and independent of the length of season.

At baseline values of the parameters, offspring sex ratio (mean lifetime proportion sons) produced by a mother was 0.57. Total investment allocated to daughters was 0.53, as

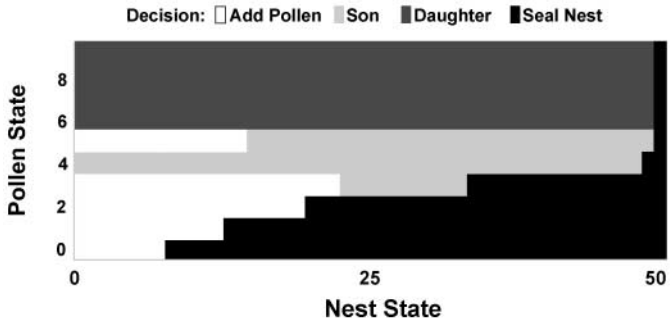


**Fig. 2.** Decision matrix example, shown at a specific time ($t = 100$). 'Pollen state' is the amount of provision (nectar and pollen together) in the current brood cell. 'Nest state' is the maternal fitness value, summed over the brood cells completed in the nest. The value of each cell is derived from Fig. 1.

**Table 2.** Sensitivity analysis for the dynamic state variable model, testing the impacts of risk and the time required to carry out various nest-building activities

| Description | Optimal size | | Male sex ratio | Nest size (# of cells) |
|---|---|---|---|---|
| | Daughters | Sons | | |
| Baseline values | 6 | 4 | 0.57 | 2.8 |
| $T = 125$ | 6 | 4 | 0.59 | 3.0 |
| $T = 500$ | 6 | 4 | 0.57 | 2.8 |
| $T = 1000$ | 6 | 4 | 0.57 | 2.8 |
| $P = 0.5$ | 6 | — | 0 | — |
| $P = 2$ | — | 4 | 1 | 2.0 |
| $P = 4$ | — | 4 | 1 | 1.4 |
| $E = 2$ | — | 4 | 1 | 5.6 |
| $E = 4$ | 6 | — | 0 | 2.4 |
| $E = 6$ | 7 | — | 0 | 1.5 |
| $S = 2$ | 6 | 4 | 0.59 | 2.7 |
| $S = 6$ | 6 | 4 | 0.62 | 3.0 |
| $S = 12$ | 6 | 4 | 0.89 | 3.4 |
| $N = 1$ | 6 | 4 | 0.50 | 1.8 |
| $N = 4$ | 6 | 4 | 0.61 | 3.1 |
| $N = 5$ | 6 | 4 | 0.85 | 3.4 |

*Note*: Sex ratio is considered the mean proportion of sons produced in a mother's lifetime. The model considers the following parameters: $T$ = total time available for the bees to build nests, $P$ = time to collect a load of pollen and nectar, $E$ = time to lay an egg of either sex and complete the brood cell, $S$ = time required to seal the nest, $N$ = time to find a new nesting site. Baselines values: $T = 250$, $P = 1$, $E = 3$, $S = 4$, $N = 3$. (Size values missing from the optimal size columns are due to no offspring of that sex being produced.)

daughters require 50% more investment than sons. Increasing the amount of time required to collect a load of pollen to provision the brood cell resulted in an increase in the proportion of sons produced (Table 2). At high pollen collection time values, only sons were produced, while low values resulted in only daughters.

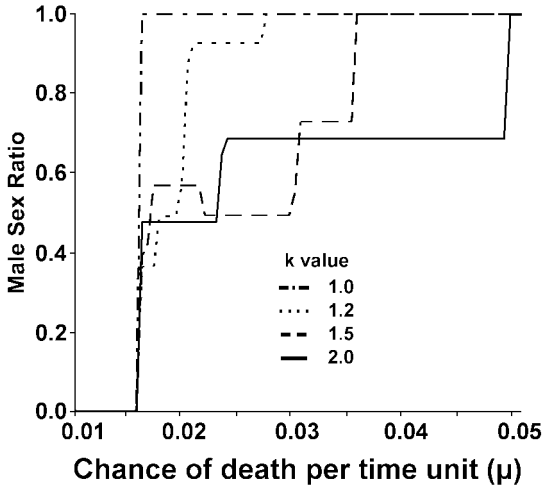


**Fig. 3.** Sex ratio of offspring produced in the forward iteration by theoretical leafcutter bees ($n = 250$), as a function of maternal mortality ($\mu$). Each line represents a different value of $k$ (proportional increase in nest value when sealed). Sex ratio is considered the average proportion of sons produced in a mother's lifetime. Other parameters were set at baseline values (see Table 2 for values).

The effect of mortality (i.e. the probability that the mother died per unit time) had an effect similar to varying the time to collect a load of pollen (Fig. 3). A high probability of mortality results in only sons being produced. Median values of $\mu$ resulted in a sex ratio of ~0.6, while low values resulted in only daughters being produced. Increased risk per unit time also resulted in nests being sealed earlier (i.e. with fewer offspring). Regarding the value of sealing the nest, higher values of $k$ moderate the effect of maternal mortality so that the production of daughters extends over a greater range of $\mu$. Higher values of $k$ also led to smaller nests, but more of them (Fig. 4).

Moderate values for the time required to locate new nesting sites resulted in a sex ratio around 0.6; this sex ratio value increased to approximately 0.9 when greater search time was required. The average number of offspring per nest increased as the time required to locate a new nest increased, while the average number of completed nests decreased.

Increasing the slope of the male maternal fitness return curve increased the proportion of sons produced but had little impact on the optimal size of male offspring. Increasing the slope of the female curve increased the proportion of daughters but, in contrast, also increased their optimal size. Changes in the slope of the curves for one sex had no impact on the optimal size of the other sex; there was simply a change in sex ratio.

To test for the generality of our insights, we also used linear offspring payoff functions that were constrained at a maximum. The general response did not change from the results using curved functions.

## DISCUSSION

Our theoretical model suggests that the decision of when to cease provisioning new offspring and perhaps engage in sealing the nest is impacted by several factors, including the current nest value, ease of obtaining resources, and risk of mortality. The benefits of the

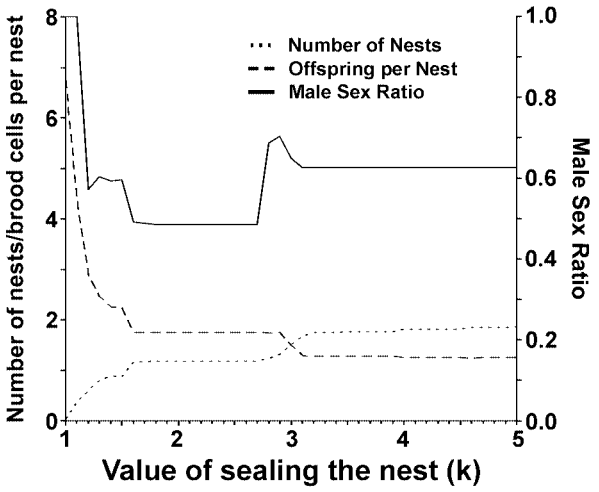


**Fig. 4.** Results of the forward iteration by theoretical leafcutter bees ($n = 250$), as a function of $k$ (proportional increase in nest value when sealed). Sex ratio is considered the mean proportion of sons produced in a mother's lifetime. Other parameters were set at baseline values (see Table 2 for values).

sealing behaviour are slightly unusual in that the main fitness gain is not related to the amount invested into the act of sealing the nest, but rather in the value of the offspring already provisioned in the nest. We found that the greater the benefit of sealing (either because of increased benefits or decreased negative impacts), the more frequently this terminal activity occurred. This is despite the fact that if the mother waited to seal until the nest contained twice as many offspring, she would gain twice the fitness from the time spent sealing the nest. This decision (accepting a smaller reward now as opposed to waiting for a bigger reward later) indicates mothers benefit more ensuring some 'extra' benefit is received from sealing (if mothers wait until the nest is very large, they may die before sealing and receive no extra sealing benefit).

In most maternal investment models, the benefits from decisions are incremented once. In other words, once fitness is accrued, for example, from one offspring, no further fitness can be accrued from that offspring in the future (e.g. once the offspring has been fledged). However, one of the unique features of the solitary bee system is the fact that a mother is able to accrue fitness first by producing offspring and later by further protecting that offspring via sealing the nest. This is a form of Clark's (1994) asset protection principle. According to Clark, the asset protection principle states that the importance of protecting the current reproductive asset increases as the value of that asset rises.

The impact of asset protection (i.e. likelihood of sealing is a positive function of nest value) can be revealed by comparing the results of the model run with and without asset protection [no asset protection ($k = 1$) = no benefit to sealing; asset protection = nest value increase with the multiplier $k > 1$]. With no asset protection, the nest is never sealed; mothers completely fill the nest with brood and produce only sons (Fig. 4). Introducing asset protection into the model results in optimal reproductive decisions being altered. As the value of $k$ increases, the number of offspring per nest quickly decreases, the number of sealed nests increases, and the proportion of daughters produced quickly increases from 0% to ~40%. The biologically realistic values of $k$ are likely in the lower portion of our tested

range ($k \geq 1$–2), although this will vary with conditions, especially chance of death to the mother and chance of brood cell parasitism.

An interesting sidebar to the asset protection concept is the emergent sex ratio of offspring, which in itself is strongly influenced by several factors. In general, the greater the investment involved in building a brood cell, the greater the proportional production of sons. This partially corroborates the idea that increasing the investment required to collect a load of resources will decrease the optimal amount of resources to invest. What we found is that the optimal offspring size does not change, but there is a proportional increase in the production of the smaller sex (males), thereby decreasing the average amount of resources invested per progeny. Optimal size only changes when the shape of the fitness function changes. In other words, factors such as pollen collection time may have an impact on offspring size, but only if the changes alter the shape of the maternal fitness returns curves. We also found that, under a variety of conditions, total investment in each sex (i.e. time) was relatively equal.

In this model, mothers were not constrained to invest equally in each sex. With extreme values of most of the parameters mothers produced all sons or all daughters. However, for median values that are within the range we might expect to find in nature, the sex ratio was around 0.6, with 6 units of pollen invested per female and 4 units of pollen per male. In nature, this range where the sex ratio value is moderate is likely greater because of the increasing value of the under-produced sex, resulting in increased selection pressure against extreme skew of the sex ratio. This lack of frequency dependence in the model is a shortcoming that should be addressed in the future.

This system where investment is impacted by two temporally separated decisions raises a number of interesting questions. How should the mother's sex ratio and sealing behaviours change as ecological conditions change? When is it better to produce sons and delay sealing in response to resource availability/adult mortality risks issues, and when is it better to produce a few daughters and seal quickly? How do the various factors influence these decisions? Our multifaceted approach appears to indicate that numerous different factors can influence the optimal sealing and offspring sex ratio decisions. The important step now is to elicit the role of the interactions between these factors both through modelling and field experiments to understand the role each plays in determining sealing decisions and sex ratio in a multifaceted world.

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