Evolutionary Ecology Research, 2010, **12**: 347–361

Egg maturation, nest state, and sex ratios: a dynamic state variable model

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ABSTRACT

Background: Parents can invest in offspring through a variety of behaviours. Optimization models of these behaviours are usually based on determination of the single 'factor' parents optimize for a given set of conditions. Interactions between factors are rarely considered.

Question: Do mothers optimize a single factor related to the investment in offspring (e.g. current nest state or mature egg state), or do mothers find an optimal balance between these two in relation to maximizing lifetime reproduction?

Methods and key assumptions: A dynamic state variable model. We develop a 'hybrid' model that examines mothers' allocation decisions to offspring by considering mature egg and nest state as well as other environmental/ecological factors. 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 determine investment in one or a few offspring within a brood but others affect the entire brood. Egg maturation rate is a constant.

Conclusions: Our results demonstrate that there is no single limiting factor; instead, there is some 'optimal balance' between mature egg and nest state that determines the optimal reproductive decision.

Keywords: dynamic state variable model, Hymenoptera, nest provisioning decisions, offspring sex ratio, optimizing multiple resources.

INTRODUCTION

Numerous allocation problems occur in a variety of organisms when disparate resources must be optimized to maximize lifetime reproduction (Hengeveld *et al.*, 2009). In a similar fashion, when state dependence impacts payoffs, there will be occasions when the state of two different resources, often requiring disparate inputs, must be co-optimized. For example, one state could impact survival whereas another could determine reproductive rate, but the resources needed to satisfy these state dependencies could vary independently. Here we examine the relationship and interrelationship between current nest state and mature egg state in relation to maximizing lifetime reproduction.

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Deducing the evolutionarily stable Fisherian sex ratio depends on the limiting factor in parental reproduction (Rosenheim *et al.*, 1996). This limiting factor becomes the 'currency' for the optimization of parental investment. Parents that optimize this limiting factor will gain the greatest lifetime fitness. For example, when food is the limiting factor, parents should maximize their fitness per unit of food allocated to offspring. Many such factors have been shown to impact reproductive fitness across a wide variety of species (Freeman *et al.*, 1980; Lloyd and Venable, 1992; Wrensch and Ebbert, 1993; Brunet and Charlesworth, 1995). Unfortunately, as noted above, there is frequently more than one limiting factor and such factors may not trade off in a simple 'either/or' fashion. When this is the case, there will be some optimal balance between reproductive factors that determine offspring allocation decisions.

In many species, this optimal determination will involve the central life-history decision on when to terminate investment in the current reproductive event. The basic assumption is that parental investment benefits show diminishing returns while at the same time investment in the current brood reduces future reproductive potential (Williams, 1966a, 1966b). The assumption is that the investment is terminated when the long-term 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.

Two key factors that impact the lifetime reproductive success of a mother are the rate at which she can mature eggs and the value of her current brood. In simple terms, all else being equal, the faster a mother can produce eggs, the more eggs she will be able to deposit during her lifetime. The value of her current (and possibly only) brood is key, as the size, number, health, protection, and so on of these offspring will determine how many of the mother's genes are passed on to the next generation. Here we develop a unifying theory using the common currency of fitness to address these two disparate but related resources, eggs and nest.

Although the 'present–future trade-off' is conceptually simple when idealized as a single, discrete event, in reality parental investment in offspring occurs through a vast array of activities. Parents obtain various types of food, build nests, defend young from predators, and keep offspring warm. These investments are often difficult to quantify, as some are directed at a single or a few offspring while others are directed at an entire brood. This complex problem has received some attention, theoretically exploring mature egg state (Rosenheim *et al.*, 1996) and nest state (Peterson *et al.*, 2007). In this paper, we develop a hybrid model that examines mothers' allocation decisions to offspring by considering mature egg and nest state as well as other environmental/ecological factors, including mortality, food accessibility, and availability of nesting sites.

We develop a dynamic state variable model (Mangel and Clark, 1988; Clark and Butler, 1999; Clark and Mangel, 2000; Alonzo, 2002) to elucidate reproductive decisions in a solitary bee where both mature egg and nest state are primary state variables in the model. Mothers make the decision on the sex of their offspring and also when to terminate one form of investment by stopping one type of investment (provisioning) and engaging in another (sealing the nest). This nest-termination decision is based on the number of mature eggs, risk of mortality, nest state, provisioning state of the current brood cell, and the availability/ease of obtaining resources. The value of sealing the nest is a result of increased protection for offspring in the nest from predators, parasites, and other threats. We find that the different nesting behaviours are easily incorporated into the above framework and considering them expands the range of interesting phenomena explained (e.g. sex order of offspring).

Oocyte production limits reproductive success in two ways over an individual's lifetime (Rosenheim *et al.*, 1996). There is both the physiological cost of egg production and the 'opportunity cost' of depleting a finite resource. The physiological cost of egg production in other insects has been shown to be high, resulting in reduced survivorship of the mother (Roitberg, 1989; Lessells, 1991; Tatar *et al.*, 1993). The result is that eggs are produced at considerable cost (Rosenheim *et al.*, 1996; Nager, 2006). The opportunity cost results from already-deposited eggs being unavailable for any future reproductive event. Egg maturation rate may be a further limiting factor in reproductive decisions (e.g. completing the nest, sex allocation) and thus has been integrated into our model. This allows us to better understand the effect of the interaction between mature egg and nest state on sex allocation decisions.

The construction of nests in solitary bees involves mothers building nests comprised of a number of brood cells, built and provisioned sequentially, with one cell being completed before the next is initiated (Freeman, 1981). The adult size of offspring is strongly correlated with the amount of pollen (we refer to pollen and nectar collectively simply as pollen) that is provisioned to the brood cell (Klostermeyer *et al.*, 1973; Bosch and Vicens, 2002). All food consumed by the developing progeny prior to adulthood is provided solely by the mother during production of that individual brood cell. Furthermore, the haplodiploid sex determination of hymenoptera allows the mother bee to completely control the primary sex ratio of her offspring, without the high costs found in other species [e.g. killing offspring of a certain sex (Burley, 1982)]. Sons and daughters are usually provisioned with different amounts of pollen, with daughters generally emerging approximately 20% larger than sons (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 all offspring when sealed in the nest. However, once the nest is sealed, time and energy must be spent searching for a new nest construction site to harbour future offspring.

We used the alfalfa leafcutter bee, *Megachile rotundata*, as our model species and parameter values were either known or determined through experimental work reported elsewhere (Peterson, 2004; Peterson and Roitberg, 2006a, 2006b). We have observed that *M. rotundata* nests are often sealed early in the season before the nest cavity is 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). Caps varied in size from 1 to 30 mm and the number of caps from zero to three (J.H. Peterson and B.D. Roitberg, unpublished data). The timing of these activities is also likely to be affected by the availability of mature oocytes (Rosenheim *et al.*, 1996).

METHODS

We combined two previous models that examined allocation decisions based on egg maturation (Rosenheim *et al.*, 1996) and nest state (Peterson *et al.*, 2007) to develop a more comprehensive investment termination behavioural model for solitary bees. Like our previous model (Peterson *et al.*, 2007), this new model examines when a bee should terminate investment in current offspring, how many offspring to produce in a nest, the sex of the offspring, and when to seal the nest. However, this model also considers the impact of egg maturation rate and its interaction with other factors. We assume that the mechanisms underlying these decisions evolved to maximize expected lifetime reproductive success.

A basic assumption of 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

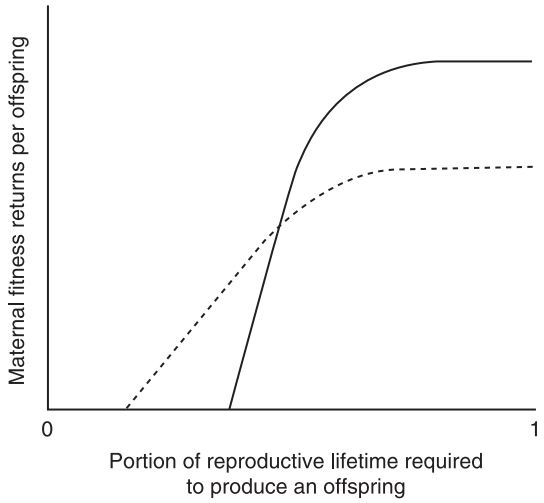

Fig. 1. Assumed cumulative maternal fitness gain is a function of the amount of time spent provisioning a single son (- - -) or daughter (—) for a given environment. Cumulative maternal fitness is considered the number of copies of alleles passed on to future generations wherein parents who invest more in an offspring generally accrue greater fitness returns from that offspring. [Both curves would reach the upper limit earlier (curves shifted left) if resources were easy to obtain, and the opposite would occur if resources were more difficult to obtain.] Daughters require greater initial investment [daughters are 20% larger than sons (Klostermeyer and Gerber, 1969; Klostermeyer *et al.*, 1973)], but increased investment yields greater fitness returns (i.e. large females are able to produce more eggs, while large males in a non-aggressive species have less benefit from increased size).

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.

Our model is heuristic. However, wherever possible, we use parameter values that closely represent natural systems. 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 (e.g. large females are able to produce more eggs while large males in a non-aggressive species have less benefit from increased size). Third, we have ignored potential population sex ratio effects on these functions (e.g. if males were rare, their value would be higher) (for more details, see Peterson *et al.*, 2007).

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:

$$f_m = -4 + (a_m(1 - e^{-(p\gamma_m)})) \tag{1a}$$

$$f_f = -6 + (a_f(1 - e^{-(p\gamma_f)})) \tag{1b}$$

where f_m is the fitness for a son (male) and f_f is the fitness for a daughter (female). The variables a_m and a_f control the asymptote of the curve of males (m) and females (f) respectively, and γ controls the slope based on the number of pollen loads (p) and the sex.

Table 1. Summary of state variables and other parameters used in our 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	200
t	Time units	(1, 200)
State variables		
$P(t)$	Current pollen value collected	(0, 9)
$V(t)$	Current nest value	(0, 49)
$E(t)$	Mature egg state	
Parameters		
μ	Chance of death per time unit	(0, 0.1)
k	Multiplier of nest value from sealing	(1, 5)
t_p	Time required to add pollen	(0.5, 2)
t_m	Time required to produce a son	(1, 5)
t_f	Time required to produce a daughter	(1, 5)
t_s	Time required to seal the nest	(1, 30)
t_n	Time required to find new nest site	(1, 10)
O_{mp}	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_{fp}	Fitness benefit for producing a daughter (f) as a function of the amount of pollen in the brood cell (p)	Based on equation (1b)

State dynamics

The three state variables in our model (Table 1) are: (1) *pollen state* (P) – the amount of provision in the current brood cell; (2) *mature egg state* (E) – the state of mature oocytes; and (3) *nest state* (V) – the total value of completed brood cells (based on size, sex, and number) in the current nest. Mothers gain fitness both from the completion of an offspring brood cell [based on the amount of pollen provision (size) and sex of that offspring] and when a nest is sealed (based on the total value of the offspring in the nest increasing by a given percentage as a result of all cells being better protected).

Two of the state variables – pollen state (P) and nest state (V) – can change independently during each time step (t) depending on the decision made by the mother. In terms of mature egg state, regardless of the decision made by the mother she matures eggs at a constant rate (E). Time is considered in discrete units (t). Within each time unit, the mother bee faces a background probability of death based on which of the following decisions she chooses:

1. Rest, the safest choice. During rest (and all other activities), eggs mature at a constant rate, e, per time unit:

$$P(t + t_r) = P(t) \tag{2a}$$

$$V(t + t_r) = V(t) \tag{2b}$$

$$E(t + t_r) = E(t) + e(t_r) \tag{2c}$$

where t_r is the time spent resting.

2. Add more pollen to the current brood cell:

$$P(t + t_p) = P(t) + 1 \tag{3a}$$

$$V(t + t_p) = V(t) \tag{3b}$$

$$E(t + t_p) = E(t) + e(t_p) \tag{3c}$$

where t_p is the time spent collecting pollen.

3. Lay a male egg (son) and complete the brood cell:

$$P(t + t_m) = 0 \tag{4a}$$

$$V(t + t_m) = V_t + O_{mp} \tag{4b}$$

$$E(t + t_m) = E_t + e(t_m) \tag{4c}$$

where O_{mp} is the increment in nest value from adding a son of pollen value (p) and t_m is the time required to deposit a male egg and close the brood cell.

4. Lay a female egg (daughter) and complete the cell:

$$P(t + t_f) = 0 \tag{5a}$$

$$V(t + t_f) = V_t + O_{fp} \tag{5b}$$

$$E(t + t_f) = E_t + e(t_f) \tag{5c}$$

where O_{fp} is the increment in nest value from adding a daughter of pollen value (p) and t_f is the time required to deposit a female egg and close the brood cell.

5. 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.

$$P(t + t_s + t_n) = 0 \tag{6a}$$

$$V(t + t_s + t_n) = 0 \tag{6b}$$

$$E(t + t_s + t_n) = E(t) + e(t_s + t_n) \tag{6c}$$

where t_s is sealing time and t_n is time to find a new nest. The act of sealing the nest results in the final fitness benefit the mother will receive from this nest. The benefit is based on the value of offspring sealed in the nest, as each offspring has increased protection. No further fitness can be gained from this nest and a new nest site must be found. Therefore, P and V take values of 0.

Terminal fitness

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

Dynamic programming equation

For this dynamic programming equation (7), Line 1, right-hand side, calculates the expected fitness from resting and amount of eggs that mature during this time. The e values in each of the following lines takes the current values of mature eggs plus the eggs that mature during

the time required to complete this decision, discounted by survival while resting $(1 - \mu_r)$. Line 2, right-hand side, is expected fitness from adding pollen and eggs matured during this time, discounted by survival while collecting pollen; Line 3, right-hand side, is current plus expected fitness from producing a son (f_m) and matured eggs, discounted by survivorship $(1 - \mu)$ during the son production process; Line 4, right-hand side, the same as above but for a daughter (f_f); and Line 5, right-hand side, is fitness from sealing the nest and maturing eggs discounted by survival while sealing plus expected fitness discounted by survival while seeking a new nest. The 'max' term refers to the decision to commit to one of the five mutually exclusive behaviours, which yields the maximum fitness value.

$$F_{\max}(p, e, v, t) = \begin{bmatrix} (1-\mu_r)\, F(p, e+e_r, v, t+t_r) \\ (1-\mu_p)\, F(p+1, e+e_p, v, t+t_p) \\ f_m + (1-\mu_m)^{t_m}\, F(0, e+e_m, v+0_{mp}, t+t_m) \\ f_f + (1-\mu_f)^{t_f}\, F(0, e+e_f, v+0_{fp}, t+t_f) \\ (1-\mu_s)^{t_s}\, vk\, (1-\mu_n)^{t_n}\, F(0, e+e_s, 0, t+t_s+t_n \end{bmatrix} \quad (7)$$

The basic parameter values were estimated when data were 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, time required to mature oocyctes, risk of adult mortality (μ), value of sealing the nest (k), time required to locate a new nest site, and the shape of the maternal fitness return curves. The many mortality factors (e.g. predators and parasitoids) were generalized into a background mortality rate that assumes there is a given chance of death for every time unit, allowing the model to be more generally applicable. As we increase this background mortality, the less likely a mother is to survive each time unit. 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 to a five-fold increase in the value of the nest.

We employed our model in two different ways. First, we used backward induction starting from $t = T$ (where all states are known) and moving back in time to determine the optimal decision for every possible set of circumstances. This process yields an optimal decision matrix. Then we employed this matrix in a forward iteration (i.e. simulation) starting at $t = 1$ with a given set of conditions and then moving forward through time before drawing the appropriate decision from the matrix.

RESULTS

In our current model, as well as in Peterson *et al.* (2007), the results showed that the greater the mortality risk (probability of death per unit time = μ), the more likely mothers are to produce sons; here we examine the point where production switches to a majority of sons. First, we examine the relationship between death rate and egg maturation rate (Table 2). Then we examine how this relationship is impacted by several other factors: pollen collection rates, time to lay an egg and complete the cell, value of sealing, sealing time, time to find a new nest, and length of season. When the chance of death per time unit is extremely high ($\mu > 0.04$), these factors have very little impact on maternal offspring-related decisions. Therefore, we focus on μ values less than 0.04 unless otherwise stated.

Table 2. Optimal decisions (sex ratio, nest size, offspring size) made under high and low egg maturation rates with low, medium, and high death rates of hypothetical mother leafcutter bees

	High egg maturation			Low egg maturation		
Chance of death:	Low	Medium	High	Low	Medium	High
Sex ratio (female)	1.0	0.5	0.0	0.5	0.0	0.0
Nest size	18	5	2	8	4	2
Offspring size, male	4	4	4	4	4	4
Offspring size, female	6	6	6	6	6	6

Death rate and egg maturation

Considering sex allocation decisions, the general relationship between the impact of egg maturation rate and death rate (μ) on sex allocation is that as the maturation rate increases, the lower the μ value before mothers switch to producing more sons than daughters (Fig. 2). Using our benchmark values, there is an almost 30% increase in μ values where mothers switch to producing a majority of sons between high egg maturation ($e = 0.10$ eggs matured per time unit) and low egg maturation ($e = 0.05$ eggs matured per time unit). This trend continues as egg maturation rates increase, until females mature eggs at a rate where they are constantly available.

Egg maturation rate impacted nest size (sealing decisions) across all variables, except when μ was extremely high (above 0.4). The lower the egg maturation rate, the more frequently the nests were sealed (i.e. fewer offspring were produced before the current nest was sealed and a search began for a new nesting site). Figure 3 shows higher egg maturation rates result in a greater number of offspring produced before the nest is sealed and also how this effect declines as μ increases.

Total cell production was double with very low μ values when comparing high (0.10) and low (0.05) egg maturation rates. This difference decreased with increasing μ values to the point where the number of cells produced was similar with very high μ values (0.04).

We now use these baseline results to examine the impact of other factors on individual variables that most impact mothers' allocation decisions. For a complete table of generalized results, see Table 3.

Pollen collection rates

Sex ratio was only impacted when pollen collection rates and egg maturation were both very low, resulting in basically only sons, even with very low μ values. Total cell production was consistently 30% greater with high compared with low egg maturation rates.

Time to lay an egg and complete the cell

The size of nests doubled with low compared with high egg maturation rates at very low μ values.

Value of nest sealing

Nest size was consistent across sealing values with low egg maturation, but with high egg maturation the size of nests at very low μ values was many times greater. This difference disappeared with even moderate μ values.

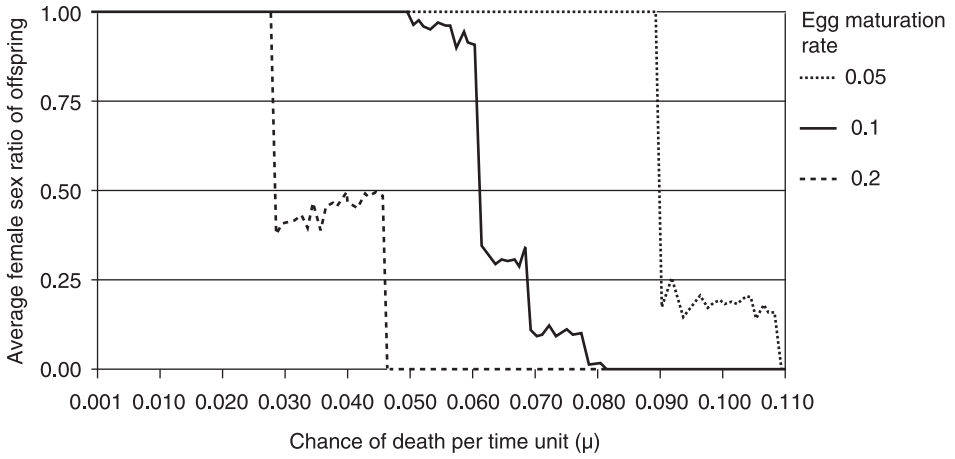

Fig. 2. Sex allocation decisions by mothers over various egg maturation rates. The slower that eggs are matured, the greater the chance of death (μ) before mothers switch to producing sons.

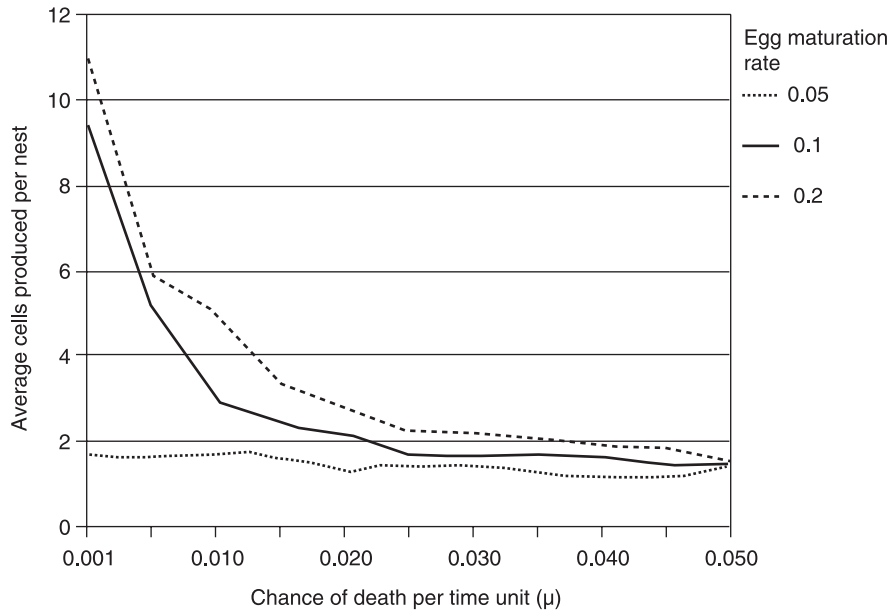

Fig. 3. Number of cells produced per nest over a variety of egg maturation rates as the chance of death (μ) increases. When eggs are slow to mature (0.05), mothers cap small nests frequently, essentially waiting for eggs to mature, resulting in smaller nests. This behaviour decreases as μ increases, to the point where all egg maturation rates produce nests of similar size.

Length of season

All season lengths demonstrated a gradual increase in nest size as the egg maturation rate increased. This increase was most significant between egg maturation rates of 0.1 and 0.2 (unlimited eggs) where the size of nest before sealing doubled. When the season is shorter, mothers tolerate a much higher μ value before switching to the production of males.

Table 3. Summary of how sex ratio, nest size, and cell production change with high and low egg maturation rates for various factors in a state-dependent foraging model for hypothetical leafcutter bees

	Sex ratio: chance of death where offspring sex switches		Nest size		Cell production	
	High egg maturation	Low egg maturation	High egg maturation	Low egg maturation	High egg maturation	Low egg maturation
Default model values (increasing chance of death)	*Lower switch to sons*	*Higher switch to sons*	*Decreasing*	*Constant*	*Greater*	*Lower*
Increasing pollen collection time	Constant	Increases subtly	Increases	Constant	Increases dramatically	Increases dramatically
Increasing time to lay egg	Increases greatly	Increases	Decreases subtly	Decreases subtly	Decreases subtly	Decreases subtly
Increasing value of nest sealing	No change	No change	Decreases	Constant	Decreases subtly	Decreases subtly
Increasing length of season from $T = 50$ to $T = 200$	Decreases greatly	Decreases greatly	Increases greatly	Increases greatly	Increases	Increases
Increasing sealing time	No change	No change	Increases	Becomes parabolic	No change	Decreases subtly
Increasing time to locate new nest	No change	No change	Increases	Increases greatly	Decreases	Decreases

Note: The sex ratio column considers the chance of death required for mothers to switch to producing a majority of sons.

Sealing time

High egg maturation rates and very low μ values resulted in mothers not sealing the nest until later, resulting in very large nests. Mothers sealed the nest earlier (i.e. with fewer offspring) when time required to seal the nest was short and the egg maturation rate was high, while nest size remained relatively constant when the egg maturation rate was low.

Time to locate a new nest

Increasing the time required to find a new nesting site, after the previous nest had been sealed, dramatically increased nest size to the point where mothers produced only one nest with very high search time to find a new nest site.

DISCUSSION

Our model deals with animals that must allocate disparate but related resources towards their offspring. The goal of previous theoretical models was to identify factors that limit lifetime reproductive success. In those models, a single limiting factor determined how mothers maximized investment. These models generally considered factors such as availability of different resources, with Rosenheim *et al.* (1996) examining egg maturation and Peterson *et al*. (2007) nest state. Depending on the conditions employed in those articles, different factors were limiting and controlled the optimal decision. Our current model takes another step towards broad applicability by considering the possibility that no single limiting 'resource' is optimized. In reality, mothers need to balance the use of multiple resources. Our current model considers all of the above factors and asks whether changes in more than one resource under a given set of conditions alter optimal decisions. Our results demonstrate that, in general, there is no single limiting factor but some 'optimal balance' between mature egg and nest state to determine the optimal reproductive decision.

Maternal investment models traditionally have the benefits from decisions incremented once. However, there are circumstances in which the investment is incremented a second (or more) time (Peterson *et al*., 2007); such is the case for many solitary bees. A mother is able to accrue fitness first by producing offspring and then add on fitness by further protecting that offspring through sealing the entrance to the nest. This is a form of Clark's (1994) asset-protection principle. The theoretical bees in both our current and previous model appear to follow this principle, as the greater the benefit of sealing the nest the more frequently this terminal activity occurred. Accepting a guaranteed smaller reward from sealing now, as opposed to waiting for a potential larger reward in the future, indicates mothers benefit more by ensuring some sealing benefit is received. In addition to these theoretical results, we have experimental evidence to support the asset-protection principle in leafcutter bees (J.H. Peterson and B.D. Roitberg, unpublished results).

While single-factor optimization models for reproduction decisions have been useful, in reality decisions are rarely controlled by a single factor. It is the interrelationship between factors that controls decisions made by organisms across a variety of situations. Considering both egg maturation rate and nest state (asset protection) allows us to examine the more realistic world where the choice may not be 'either/or' but some optimal balance. In our unifying model, using the common currency of maternal fitness to address the impact of various states we found that a balance between factors determined optimization. Comparing the results of our model for an egg maturation rate of 0.05 and the time to

collect a unit of pollen (t_p) is 1 versus 2, the female sex ratio drops below 50% at $\mu = 0.046$ and $\mu = 0.019$ respectively, suggesting that pollen collection is the limiting factor. However, when we compare the difference between these pollen collection rates with a higher egg maturation rate (0.10), these same μ values are 0.036 and 0 respectively. Examining the four vastly different μ values means that both the egg maturation rate and the pollen collection time alter the optimal decisions in a non-linear fashion. There is no single limiting resource; there is an optimal trade-off between various resources.

Our results demonstrate that the lower the egg maturation rate, the fewer offspring are produced before the nest is sealed. Asset protection is employed with smaller nests when the time to mature an oocyte is greater. In this context, time spent sealing the nest is not so much 'lost time' as eggs are matured during this time, and the mother's only other option may be to rest when she has no mature eggs ready.

In general, high death rates ($\mu > 0.4$) tend to override all other factors in influencing maternal decisions (e.g. Fig. 3). At lower μ values, many factors impact nest size as we observed previously: time required to provision a brood cell, risk of adult mortality, value of sealing the nest, time required to locate a new nest site, and the shape of the maternal fitness return curves (Peterson *et al.*, 2007). When we considered egg maturation rates and μ, we found that lower egg maturation rates generally muted or even eliminated the impact of these factors. At high egg maturation rates, the size of the nests increased as μ decreased, as we found previously. Low egg maturation rates masked other effects and the size of nests remained consistent across μ values.

Considering sex allocation decisions specifically, our theoretical model demonstrates complex interactions between egg maturation rates and death rates. However, in general, the more dangerous the environment, the more likely mothers are to produce the cheaper sex, in this case sons. However, the lower the maturation rate, the greater the risk of death before production shifted to sons. In other words, as egg maturation becomes a more limiting factor, the probability of producing a daughter increases. In extremely low egg maturation systems, the amount of time spent provisioning the cell is less important, as the mother will have to wait even after the cell is provisioned for an oocyte to mature so that she can deposit the egg and complete the brood cell. This waiting behaviour is frequently seen after provisioning is completed on one cell and before a provisioning a new cell begins (J.H. Peterson and B.D. Roitberg, unpublished data).

There is an upper maximum above which further increases in the maturation rate do not impact decisions. Above this point the mother essentially always has a mature egg ready to deposit and therefore egg maturation is no longer a factor in allocation decisions. At the other extreme, where mature oocyctes are extremely limited, eggs may become the only factor determining allocation decisions. Given our proposed maternal fitness curves (Fig. 1), mothers who must spend time waiting for oocyctes to mature will gain more fitness per unit time by producing a large daughter than by either producing a larger son or a small son and spending the remainder of the time resting in the nest. The exception to the latter would be when the environment is extremely dangerous and resting in the nest is very safe. Under these conditions, mother may choose to produce a small male. Not withstanding these specific circumstances, the production of females when maturation rates are slow returns the greatest maternal fitness per unit time. However, a single factor does not control the best decision, as in the 'multifaceted parental investment model' (Rosenheim *et al.*, 1996). There is an interaction between multiple factors, which determines the most profitable decision.

Comparing decisions across a variety of μ values for scenarios where the total time (T) is 200, versus $T = 50$, results in a dramatic shift when the chance of death was low. When egg maturation rate was low, the μ value at which females switched to the production of sons when $T = 50$ was extremely high ($\mu = 0.090$) compared with $\mu = 0.044$ when $T = 200$. To put this into perspective, at a μ value of 0.09 a mother stands only a 50% chance of surviving to produce a single daughter. Increased egg maturation rates decreased this difference between long and short seasons such that when eggs were basically unlimited, the μ value at which mothers switched to the production of sons was similar.

When pollen can be collected quickly, there is almost no impact of egg maturation rate on offspring sex ratio. However, as the pollen collection time increases, the μ values at which females switch to the production of sons become much lower with a high egg maturation rate. Increased pollen collection time is likely to occur later in the season when available resources are further from the nest; it is also later in the season when mothers are far more likely to produce sons (Rothschild, 1979). Doubling the time required to obtain pollen from the baseline value resulted in a switch to sons at an even lower μ value, and with a high egg maturation rate mothers never produced more than 30% females and quickly switched to all males as μ increased above zero. Our results at extreme values were congruent with results for a single limiting resource, although at many intermediate values there was an interaction between factors that impacted the optimal decision in these situations.

Although we have focused on solitary bees as our example species, the issue of dealing with multiple states and optimal balance is important across numerous groups. Blood-feeding mosquito mothers do not choose a single resource to optimize but make foraging decisions that explicitly consider the trade-offs between blood feeding, sugar feeding, and oviposition (Ma and Roitberg, 2008). In *Aphytis melinus*, there is a strong interaction between the influences of host feeding and honey feeding on lifetime reproductive success (Heimpel *et al.*, 1997). For parasitoids, the host organism supplies both an egg-laying site and the egg-laying nutrients; however, sugar sources such as floral nectaries are spatially separate (Bernstein and Jervis, 2008). Belovsky *et al.* (1989) considered predator–prey interactions such as bats hunting insects and snakes foraging on frogs. This work demonstrated that considering foraging in more realistic (i.e. complex) environments, simple predictions of single-diet preferences disappeared in favour of multifaceted wide-ranging diets. These examples demonstrate that the interaction between factors, as opposed to simply determining a single factor to optimize, is key to understanding numerous behaviours.

Our unifying model facilitates examination of optimal decisions among a variety of disparate resources. Using the common currency of fitness in this model to address the impact of various states demonstrates that optimal decisions were not simply a matter of finding the limiting factor, but a trade-off between multiple limiting factors. Many examples where two different variables were modified demonstrate that each of the four combinations resulted in different optimal decisions, such as altering pollen collection time and egg maturation rates. Not only is more than one factor being optimized, as conditions become more extreme one factor can become more influential. Lower egg maturation rates muted the impact of other factors and nest size varied little, whereas with high egg maturation rates nest size increased with decreased risk. We also found that mothers who must spend time waiting for oocyctes to mature or have shorter maximum life spans gain the most fitness by producing daughters. A single factor does not control the best decision; an interaction between multiple factors determines the most profitable decision.

ACKNOWLEDGEMENTS

We thank NSERC Canada for an operating grant to B.D.R. and a PGS-D Scholarship to J.H.P. We thank Elizabeth Elle and Dov Lank for discussions on this issue, Brian Ma for coding help, and Alex Chubaty and Derek Roff for comments on an earlier draft of the manuscript.

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