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Optimal maternal investment in the dung beetle *Onthophagus taurus*?

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Abstract Optimal investment theory is based on the assumption that the proximate constraint acting on parental investment is resource based. A trade-off between per offspring investment and total investment seems intuitive. Consequently, a parent's investment strategy is expected to represent a trade-off between the benefits of investment for current offspring and the costs to future reproduction for parents. In this study, we provide clear evidence that the costs and benefits of maternal provisioning in the dung beetle *Onthophagus taurus* influence the amount of provisions provided by the mother. Horse dung is typically of a higher nutritional value than cow dung and females were shown to provide 20% less dung to offspring when provisioning with horse dung. By reducing their investment per offspring and exhibiting a clear preference to provision offspring with horse dung, females were able to produce significantly more offspring. Females provisioning with horse dung received greater fitness returns per unit of investment and experienced lower provisioning costs, in terms of the minimum amount of dung required to produce a surviving offspring, than females provisioning with cow dung. Females provisioning in soil of low moisture content were found to have higher tunneling costs than those provisioning in soil of high moisture content, while the fitness returns per unit of investment did not differ. We adopted a marginal value theorem (MVT) approach to calculate the theoretical optimal level of investment for each dung type

and for each soil moisture. Predicted levels of provisioning were lower for horse dung than for cow dung and for moist soil than for dry soil. Therefore, the results of this study are in qualitative agreement with MVT predictions and provide empirical support for the proposal that females can adaptively adjust their level of investment in response to resource and/or habitat quality. However, the theoretically predicted optimal investment yielded a poor quantitative fit with our observed levels of investment, with females providing over twice the investment predicted by the MVT approach. We suggest that this difference may reflect either our inability in directly quantifying all the necessary costs and benefits of investment in *O. taurus* and/or the applicability of the underlying assumptions of MVT.

Keywords *Onthophagus taurus* · Parental care · Resource quality · Habitat quality · Optimal investment strategies

Introduction

Parental investment is critical for offspring growth and survival so that parent's should be expected to maximize their investment in each offspring (Clutton-Brock 1991). However, resources are often finite, so that the larger the investment made per offspring, the fewer the number of offspring that can be produced. Consequently, a parent's investment strategy is expected to represent a trade-off between the benefits of the investment to individual offspring and the costs to future reproduction (Clutton-Brock 1991).

In their seminal analysis of this trade-off, Smith and Fretwell (1974) presented a graphical model where they assumed that the survival of a given offspring required a certain minimum level of investment, and that offspring fitness shows diminishing returns with increasing investment. They concluded that an optimal level of parental investment should exist and that parental fitness should be maximized by a single level of investment in all offspring.

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Investment below the optimum should result in offspring survival being too low, and investment above the optimum should result in the production of too few offspring. Thus, the amount of investment provided to each offspring is seen as the product of stabilizing selection operating around some optimal level of investment (Smith and Fretwell 1974). A number of theoretical extensions to Smith and Fretwell's (1974) model have provided support for a single optimal level of investment (Brockelman 1975; Charnov 1976; Maynard Smith and Hoekstra 1980), even when factors such as developmental constraints (Parker and Begon 1986), multiple resources (McGinley and Charnov 1988) and variation in the availability of resources experienced during investment (Lloyd 1987; McGinley et al. 1987) are incorporated. A particularly interesting finding of McGinley et al.'s (1987) model is that the highest fitness returns should always be achieved when parents are capable of assessing and/or predicting environmental quality and thus are able to adjust their investment accordingly.

A major criticism of Smith and Fretwell's (1974) model is that it assumes that the relationship between offspring fitness and parental investment is constant throughout the environment, an assumption that is not always biologically realistic (see McGinley et al. 1987; García Dorado 1990). In reality, the trade-off is likely to represent a complex interaction between various factors, such as environmental uncertainty, predation pressure and the extent of resource competition (Brockelman 1975; Parker and Begon 1986; McGinley et al. 1987). Theoretical models incorporating the effects of environmental heterogeneity on parental investment strategies have yielded conflicting results (Kaplan and Cooper 1984; McGinley et al. 1987; García Dorado 1990). Kaplan and Cooper (1984) have shown that in a temporally unpredictable environment, a mixed strategy that occurs randomly and independently across individuals (adaptive coin-flipping), may confer fitness advantages and promote variable investment strategies. Likewise, Bull (1987) used population genetic models to demonstrate that at the population equilibrium, a given amount of variance may be maintained if this variance is derived exclusively from the environment. Furthermore, García Dorado (1990) demonstrated that although a monomorphic evolutionary stable strategy (ESS) for constant investment was the most common outcome, if an offspring receiving the optimal level of investment in one niche was unable to survive in the alternate niche, then a polymorphic strategy would invade that favours variable investment.

Empirical studies have revealed great diversity in the way that parental investment strategies covary with environmental conditions (reviewed by Bernardo 1996). Some studies have reported an increased variance in investment in unfavourable environments (e.g. Harper et al. 1970; Janzen 1977; Capinera 1979; Kaplan 1980; Crump 1981, 1984; Stamp and Lucas 1983; Thompson 1984), while others have demonstrated that mean levels of investment increase in unfavourable environments (e.g.

Kerfoot 1973; Wootton 1979; Kolding and Fenchel 1981; Reznick and Endler 1982; Brody and Lawlor 1984). Nevertheless, such studies are generally correlational and fail to directly quantify the costs to parents and the fitness gains received by offspring developing in different environments. As such, there may often be alternate hypotheses to account for the observed trends (Clutton-Brock 1991; Bernardo 1996). Therefore, to convincingly demonstrate adaptive covariation between parental investment strategies and environmental conditions, it is essential to consider both the costs and benefits of providing variable investment and the extent to which these vary with ecological conditions (Clutton-Brock 1991).

In the onthophagine dung beetle *Onthophagus taurus*, females provision offspring by removing portions of dung and packing them into the blind ends of tunnels that have been excavated beneath the dung pad (Hunt and Simmons 1998a). A single egg is deposited into an egg chamber and sealed and no further care is provided. Each egg and its associated dung provision constitutes a brood mass (Halfpenny and Edmonds 1982) and represents the entire resource base that is available to the developing larvae. Thus, the amount of investment provided to each brood mass is a major determinant of offspring phenotype (Hunt and Simmons 1997, 2000) and subsequent fitness (Hunt and Simmons 2001; Hunt et al. 2002), and is expected to be subject to natural selection.

In the southwest of Western Australia, *O. taurus* readily colonize the dung of both horse and cattle and reproduce on a variety of soil types over their wide geographic distribution. Numerous studies have demonstrated that both dung quality (Moczek 1998) and soil type (Barkhouse and Ridsdill-Smith 1986; Sowig 1996) are important factors influencing offspring provisioning in onthophagine dung beetles. For example, Moczek (1998) found that female *O. taurus* provisioning with horse dung produced significantly lighter brood masses, and Sowig (1996) found that female *O. vacca* produced significantly heavier brood masses in comparatively dry soil compared with wet soil. Both studies suggested that the observed plasticity in levels of maternal investment may represent an optimal strategy to maximize parental fitness and thus reflect differences in the costs and/or benefits associated with provisioning offspring in different habitats. As Onthophagine dung beetles provision offspring sequentially, investment in one brood mass prevents investment in additional offspring, thus providing an ideal situation to empirically test ideas relating to optimal investment strategies.

In this study we examine the costs associated with maternal provisioning on different dung types and soil varying in moisture content, and how offspring growth rates (and thus fitness gains) vary per unit of investment. We estimate the parameters necessary for a marginal value theorem approach in order to predict how maternal provisioning should vary with dung type and soil moisture. Finally, we compare our theoretically calculated optima with observed levels of investment by females.

We discuss our findings in relation to optimal investment theory.

Methods

General procedures

Onthophagus taurus were collected using baited pit traps from Margaret River in the southwest of Western Australia (Hunt et al. 1999). Beetles were maintained in the laboratory in mixed sex cultures for 2 weeks with constant access to fresh cow dung to ensure that all beetles were reproductively mature and mated prior to experimentation. The pronotum widths of all males and females used in experiments were measured using digital calipers. All experiments and rearing of offspring were undertaken in a constant temperature room set at 25°C with a 14L:10D light regime.

The horse and cow dung used in the dung quality experiments were collected from a property in the Swan Valley, approximately 25 km northeast of Perth, Western Australia. Both horses and cows occupied the same paddock and were not provided with supplementary feed and had not been drenched for at least 100 days prior to the collection of dung. Approximately 120 l of both dung types were collected and both types were individually homogenized using an industrial cement mixer. The dung was packaged into 1-l containers and frozen prior to use in experiments. The cow dung used in the soil moisture experiments was collected from a commercial dairy in Oakford, approximately 60 km southeast of Perth, Western Australia. Approximately 300 l of cow dung was collected, homogenized and frozen in individual 1-l containers, as outlined above.

We experimentally manipulated the moisture content of soil to produce two treatments: high and low soil moisture. A total of twelve 60-l plastic tubs containing moist soil were desiccated for 3 weeks in a constant temperature room set at 25°C. Half of the tubs were randomly allocated to the high soil moisture treatment where we added 6 l of water to each tub (10% water content). The other half were allocated to the low moisture treatment in which we added 3 l of water to each tub (5% water content). The sand in each tub was homogenized in a cement mixer, replaced in the original tub and sealed with a lid to ensure that water did not evaporate from the sand prior to use in experiments.

The Marginal Value Theorem approach

A frequently used method for exploring the adaptive significance of parental care decisions is to examine the costs and benefits of marginal increments in the allocation of resources by a parent; an approach referred to as the marginal value theorem (MVT) (Charnov 1976). In MVT the fitness gains (W) from engaging in an activity, such as foraging at a patch or provisioning an offspring, depend on how long an animal spends in the activity (t). Fitness gains are expected to show exponentially diminishing returns described by the gain function (e.g. Parker and Stuart 1976):

$$W(t) = W_{\max}[1 - \exp(-rt)] \quad (1)$$

where r = the rate at which W rises to its asymptote, W_{\max} . MVT predicts that the optimal time spent in an activity (t^*) will occur when the marginal gains fall below those expected from the habitat as a whole (Charnov 1976). In the case of offspring provisioning, this will occur when the marginal gains of provisioning a given offspring fall below those received by provisioning a subsequent offspring.

The optimum, t^* , can be found graphically by constructing the tangent from a point that represents the cost, C , associated with moving to a new patch or beginning to provision a new offspring, to the gain curve (Fig. 1). Alternatively the optimum can be approximated mathematically using the equation (Stephens and Dunbar 1993):

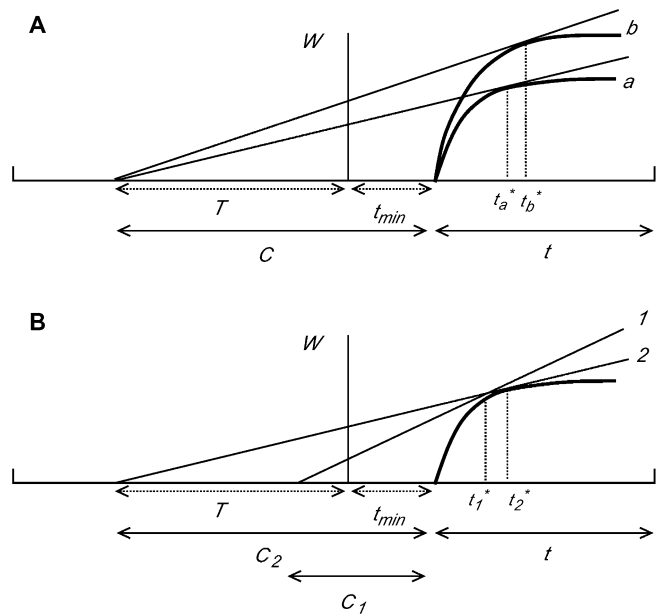


Fig. 1A, B Graphical representation of the Marginal Value Theorem. **A** Two gain curves are shown. In curve *a*, the fitness gain (W) rises more slowly with time (t) and has a lower asymptotic fitness (W_{\max}) than in curve *b*. Assuming a fixed total time cost (C) the tangent to gain curve *a* predicts a lower optimum (t^*) than the tangent to gain curve *b* because of the greater rate of fitness gain. **B** Increasing C (from C_1 to C_2) will have the effect of increasing t^* for any given gain curve because the tangent of the line will intersect the curve at a higher value of t . In our analysis of parental provisioning in *Onthophagus taurus*, and in theoretical models of parental investment, it is assumed that a parent has some minimum investment, t_{\min} , that must be made in order to produce an offspring. The total cost, C , is therefore $T + t_{\min}$ (see text for more details)

$$t^* \approx \frac{1}{r} \left[\ln(rC + 1) + \frac{\ln(rC + 1)}{rC + 1} \right] \quad (2)$$

Thus t^* is only influenced by r and C . Increasing C is predicted to increase the optimum while increasing r is predicted to reduce the optimum (Fig. 1) (Charnov 1976; Parker and Stuart 1976; Lloyd 1987; McGinley et al. 1987; Winkler and Wallin 1987; Stephens and Dunbar 1993).

In the case of maternal investment in *O. taurus*, time (t) will be the provisioning time during which females collect dung and pack it into the brood mass. We know that offspring size increases with the amount of dung provided in the brood mass (Hunt and Simmons 1997, 2000), and that both male reproductive fitness (Hunt and Simmons 2001) and female fecundity and survival (Hunt et al. 2002) increase with body size. Thus, we used offspring size as our indirect measure of offspring fitness (W). We experimentally increased and decreased the weight of brood masses provisioned on each dung type and soil moisture content (experiment 1) to determine the fitness gains received by offspring. We then used behavioural observations to convert the weight of a brood mass provisioned on each dung type and soil moisture content (experiment 2) to a provisioning time. Our MVT approach assumes that females experience a time cost when constructing a breeding tunnel (T) and we directly quantify these costs for each dung type and soil moisture content in experiment 2. Following Smith and Fretwell (1974), we also assume that there will be a certain minimal level of provisioning that is necessary to ensure that an offspring can successfully develop (t_{\min}). We quantify these costs by experimentally reducing brood mass weights above and below the survival threshold on each dung type and soil moisture content (experiment

3). Thus, we assume that the total cost of provisioning (C) experienced by a female will equal $t_{\min} + T$ (see Fig. 1).

Using each of these cost and benefit parameters, we then employ MVT to calculate the theoretically predicted optimal level of time that females should spend provisioning offspring on each dung type and soil moisture content. In an independent set of experiments, we then quantify the observed level of provisioning that females provide on each dung type and soil moisture content (experiment 4) and compare these with our theoretically predicted levels. In a final experiment we determine whether female beetles demonstrate a preference for provisioning with high quality horse dung over low quality cow dung (experiment 5).

Costs and benefits of maternal investment

Experiment 1: fitness gains per unit of provisioning (W)

To examine the relationship between provisioning and offspring size on each of the dung types, 400 randomly selected females were established in independent breeding chambers (PVC piping 25 cm in length and 6 cm in diameter). Half were provided with 250 ml of horse dung and half with 250 ml of cow dung. Chambers were maintained for 1 week, sieved and brood masses collected. Excess sand was removed and brood masses were manipulated by either adding or subtracting dung, or left unmanipulated (see Hunt and Simmons 1997). Brood mass manipulation permitted brood mass weights to be extended beyond the natural range in order to construct complete gain curves. All brood masses were individually weighed, buried in moist sand in individual plastic containers (9×9×5 cm) and maintained until adult beetles emerged. On emergence, the hatching success of each brood was recorded, and for surviving offspring, pronotum width was measured using digital calipers. Obviously, we were unable to determine dry brood mass weight when it was necessary to collect resultant offspring.

To examine the relationship between provisioning and offspring size on high and low soil moisture, 400 randomly selected females were established in independent breeding chambers. Half were provided with high soil moisture and half with low soil moisture. Each chamber was three quarters filled with the respective soil type and provided with 250 ml of cow dung. Chambers were maintained for 1 week, sieved and brood masses collected. Excess sand was removed and brood mass weight was manipulated as outlined above. All brood masses were individually weighed, buried in individual containers of sand of the same moisture as they were constructed in, and maintained until adulthood. On emergence, the pronotum widths of males and females were measured using digital calipers.

Experiment 2: the cost of constructing a breeding tunnel and relating brood mass weight to a provisioning time

Prior to the provisioning of dung into a brood mass, a female must construct a breeding tunnel beneath the dung pad. To examine the time costs associated with constructing a breeding tunnel (T) we observed females in glass "ant farms" (see Hunt and Simmons 2002). We three quarters filled each ant farm with moist sand and provided them with either 50 ml of horse dung or 50 ml of cow dung. A single, randomly selected female was then added to each chamber. Female behaviour was recorded using a time-lag video recorder (Sony SVT-124P) via a Sony CCT video camera (XC-999P) fitted with a wide-angle lens (VCL-03S12XM). All recordings were made under dim lighting in a constant temperature room at 25°C, and at a tape speed of 10 frames/s. The time taken to construct a breeding tunnel was defined as the time from when a female started moving sand to form a tunnel until the first portion of dung was packed into the brood chamber. In addition, we also measured the length of the breeding tunnel that was constructed. A total of 22 females were recorded on each dung type.

To directly compare the fitness gains with the costs of maternal provisioning it is necessary to measure the costs and benefits in the

same currency (Stephens and Dunbar 1993). Thus, we determined the time required to provision a brood mass of given weight on horse and cow dung for the 22 females video recorded above. The time taken to provision a brood mass (t) was defined as the time from when the first portion of dung was packed in the brood chamber until the brood chamber was completely sealed with dung and the female had begun covering the brood mass with sand. Once a brood mass had been completed, it was removed from the observation chamber, excess sand removed with a dissecting probe and weighed to the nearest 0.01 g with an electronic balance.

The time costs associated with constructing a breeding tunnel was estimated for females on high and low soil moisture following the protocol outlined above. A total of 20 randomly selected females were recorded for each soil moisture content. Likewise, the time required to provision a brood mass of given weight on high and low soil moisture was estimated following the protocol outlined above for the 20 video recorded females.

Experiment 3: minimum level of provisioning

To estimate the minimum amount of provisioning that is required to successfully produce an offspring on both horse and cow dung, 100 randomly selected females were established in independent breeding chambers, half with horse dung and half with cow dung. Chambers were maintained for 1 week, sieved and brood masses collected. Excess sand was removed and 102 randomly selected brood masses produced on each dung type were manipulated by removing dung so that they weighed between the 0.3 and 0.75 g. Brood masses were buried in moist sand in individual containers and maintained until hatching. After all beetles had emerged, hatching success of each brood mass was recorded and offspring size measured for those beetles that emerged successfully.

To estimate the minimum amount of provisioning required to successfully produce an offspring on both high and low moisture soil, 100 randomly selected females were established in independent breeding chambers, half with high moisture soil and half with low moisture soil, and provided with 250 ml of homogenized cow dung. Chambers were maintained for 1 week, sieved and brood masses collected. Excess sand was removed and 100 randomly selected brood masses produced on each soil type were manipulated as outlined above. Brood masses were buried in soil of the corresponding moisture content, in individual containers and maintained until hatching. Offspring size and hatching success was also measured as outlined above.

Experiment 4: observed provisioning strategies

To examine the level of investment provided by females provisioning on horse or cow dung, we measured the pronotum widths of 140 randomly selected females using digital calipers. These females were established in independent breeding chambers, three quarters filled with moist sand (~8% water content) and 250 ml of dung. Half of the females were provided with 250 ml of horse dung and half with 250 ml of cow dung. Chambers were maintained for 1 week, sieved and the brood masses collected. The chambers were then re-established for a second week of breeding in which the female was given the alternate dung type. For brood masses produced in both weeks, excess sand was removed using a dissecting probe and brood masses were dried to constant weight at 60°C. After drying, any remaining sand was removed and all brood masses were counted and weighed to the nearest 0.01 mg. Female size did not differ significantly with regard to the order that the dung was provided ($t=1.10$, $df=85$, $P=0.27$) and only females producing multiple brood masses on both dung types were included in the pair-wise analysis ($n=86$). Our pair-wise approach controls for any potentially confounding co-variation between individual responses to variation in dung type.

To examine the level of investment provided by females when provisioning in soil that varied in moisture content, we established two soil moisture treatments; high and low soil moisture. The

pronotum widths of 100 randomly selected females were measured using digital calipers. Females were established in independent breeding chambers, half containing high moisture soil and half low moisture soil, and 250 ml of homogenized cow dung. The chambers were maintained for 1 week, sieved and brood masses collected. Excess sand was removed from brood masses and brood masses were dried to a constant weight and then weighed. Female size did not differ with regard to the treatment they were assigned ($t=0.11$, $df=98$, $P=0.91$).

Experiment 5: female preference for dung quality

To examine whether females prefer to provision offspring with horse or cow dung, 20 replicate populations were established where females were given access to both dung types to provision offspring. Each replicate consisted of six females placed in a single plastic bucket (26 cm height \times 28 cm diameter), three quarters filled with moist sand and provided with 1 l of horse dung and 1 l of cow dung. Populations were maintained for 1 week and then sieved and brood masses collected. The number of brood masses produced on each dung type were counted for each of the 20 replicate populations.

Results

Costs and benefits of maternal investment

Experiment 1: fitness gains per unit of provisioning

We converted wet brood mass weight to a provisioning time and related this to the body size of offspring produced. Using equation 1 we then determined W_{\max} and r for the relationship between provisioning time and offspring size for each of the dung types. The gain curves differed between the dung types; both the asymptotic size (W_{\max}) and the rate at which offspring size increased to this asymptote (r) were greater when females provisioned with horse dung [$W_{\max}=4.90$ mm (95% confidence limits: 4.86, 4.93); $r=0.0063$ mm/min (0.0061, 0.0066), $n=657$] than when they provisioned with cow dung [$W_{\max}=4.45$ mm (4.41, 4.45); $r=0.0058$ mm/min (0.0055, 0.0061), $n=579$] (Fig. 2A).

In contrast, the gain curves did not differ with soil moisture, with both W_{\max} and r being comparable when females provisioned with low moisture soil [$W_{\max}=5.10$ mm (5.03, 5.17); $r=0.0034$ mm/min (0.0032, 0.0036), $n=615$] and high moisture soil [$W_{\max}=5.10$ mm (5.04, 5.16), $r=0.0033$ mm/min (0.0031, 0.0035), $n=592$] (Fig. 2B).

Experiment 2: the cost of constructing a breeding tunnel and relating brood mass weight to a provisioning time

We examined the time costs associated with constructing a breeding tunnel using a one-way ANOVA, with dung or soil type as the main effect and construction time as the dependent variable. The time taken to construct a tunnel did not differ with dung type ($F_{(1,43)}=0.0006$, $P=0.99$), nor did tunnel length ($F_{(1,43)}=0.63$, $P=0.43$). Therefore, we used the pooled mean across the two dung types to

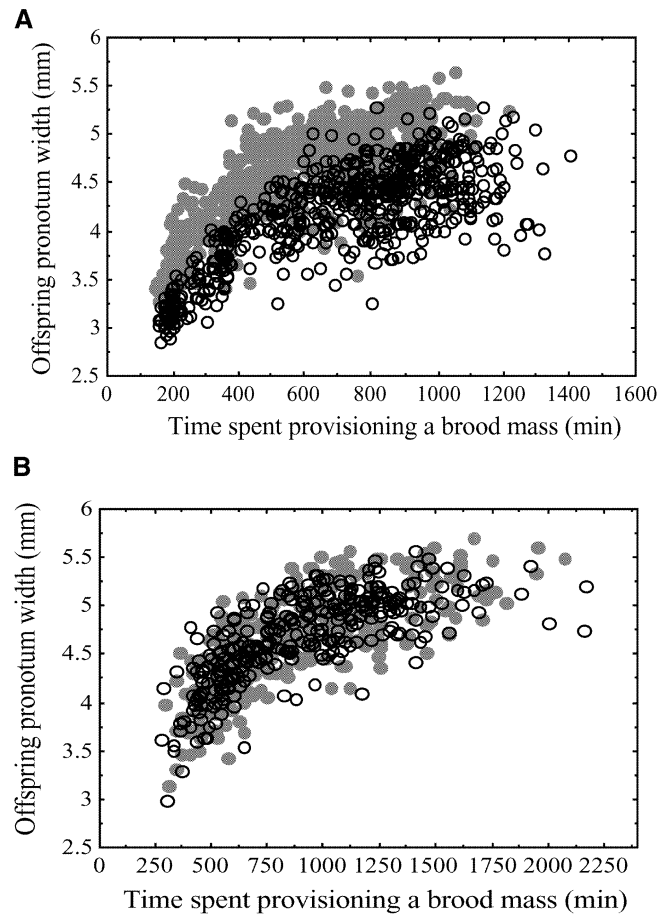


Fig. 2 **A** The relationship between the time taken to construct a brood mass (per offspring investment) and offspring pronotum width (offspring fitness) for offspring developing on horse dung (closed symbols) and cow dung (open symbols). **B** The relationship between the time taken to construct a brood mass and offspring pronotum width for offspring developing on high soil moisture (open symbols) and low soil moisture (closed symbols)

estimate the average time cost of constructing a breeding tunnel (364.44 ± 15.83 min).

In contrast, the time taken to construct a tunnel significantly differed with soil moisture ($F_{(1,39)}=43.42$, $P<0.0001$), with females taking over twice as long to construct a breeding tunnel in low moisture soil (369.23 ± 27.45 min) than in high moisture soil (180.11 ± 8.37 min). This occurred because females constructing a breeding tunnel in low moisture soil dug significantly longer tunnels (17.48 ± 0.41 cm) than in high moisture soil (9.63 ± 0.36 cm) ($F_{(1,39)}=209.69$, $P<0.0001$).

To determine the time taken to provision a brood mass of known wet weight for each dung type, we performed an ANCOVA with dung type as the main effect, provisioning time as the covariate and brood mass weight as the dependent variable. There was a significant effect of dung type ($F_{(1,42)}=99.84$, $P<0.0001$), provisioning time ($F_{(1,42)}=522.77$, $P<0.0001$), and a significant interaction between dung type and provisioning time ($F_{(1,42)}=46.34$, $P<0.0008$), on the weight of the brood mass produced.

The significant interaction term suggests a difference in the slope relating provisioning time to brood mass weight across dung types, so we calculated independent regression slopes for each dung type. To calculate these slopes, we set the Y intercept to zero on the premise that a female not provisioning a brood mass would not incur any time costs. The slope of the relationship between provisioning time and brood mass weight was $b=0.0032\pm0.00018$ g/min for cow dung ($r^2=0.88$) and $b=0.0027\pm0.000049$ g/min for horse dung ($r^2=0.95$). Thus, longer provisioning times produced heavier brood masses on both dung types, although, for a given unit of time, females were able to provide more dung to brood masses when using cow dung than when using horse dung. These slopes were used to scale brood mass weight to a provisioning time for our MVT analysis.

To determine the time taken to produce a brood mass of known weight on high and low soil moisture, we similarly performed an ANCOVA using soil moisture as the main effect, provisioning time as the covariate and brood mass weight as the dependent variable. The only significant effect on brood mass weight was the covariate provisioning time, with longer provisioning times yielding heavier brood masses (soil moisture: $F_{(1,39)}=0.01$, $P=0.91$; provisioning time: $F_{(1,39)}=494.75$, $P<0.0001$; soil moisture \times provisioning time: $F_{(1,39)}=1.12$, $P=0.30$). The lack of significance of the interaction term suggests a common slope relating provisioning time to brood mass weight for both soil types. Thus, we calculated the common regression slope across soil types, again setting the Y intercept to zero. The common slope of the relationship between brood mass weight and provisioning time was $b=0.0027\pm0.00005$ g/min ($r^2=0.90$). Similarly, we used this common regression slope to scale brood mass weight to provisioning time for our MVT analysis.

Experiment 3: minimum level of provisioning

To estimate the minimum level of provisioning required to produce a viable offspring, we performed a logistic regression analysis with the weight of manipulated brood masses as the independent variable and survival (0 or 1) as the dependent variable for each dung type. There was a significant effect of brood mass weight on the survival of offspring reared on both horse ($\chi^2=59.13$, $df=1$, $n=102$, $P<0.0001$) and cow dung ($\chi^2=105.41$, $df=1$, $n=102$, $P<0.0001$); offspring developing in smaller brood masses on both dung types were less likely to survive. The predicted brood mass weight yielding a survival probability of 0.95 was defined as our minimum brood mass weight. This value was considerably lower for horse dung [0.38 g (95% confidence limits: 0.36, 0.40)] than for cow dung [0.49 g (0.47, 0.51)]. This corresponds to a t_{\min} value of 140.89 min when provisioning on horse dung and 154.63 min when provisioning on cow dung.

Likewise, there was a significant effect of brood mass weight on the survival of offspring reared in both low ($\chi^2=39.71$, $df=1$, $n=100$, $P<0.0001$) and high moisture soil

($\chi^2=26.42$, $df=1$, $n=100$, $P<0.0001$), with offspring developing in larger broods having a clear survival advantage. The predicted brood mass weight yielding a survival probability of 0.95 was lower on high moisture soil [0.42 g (0.39, 0.45)] than low moisture soil [0.45 g (0.42, 0.48)]. This corresponds to a t_{\min} value of 168.07 min when provisioning on low moisture soil and 156.86 min when provisioning on high moisture soil.

In addition, we also examined the effect that natural variation in brood mass weight had on offspring survival for the unmanipulated brood masses in experiment 1. The survival of offspring on both horse and cow dung was not significantly related to natural variation in brood mass weight (horse dung: $\chi^2=2.03$, $df=1$, $n=300$, $P=0.16$; cow dung: $\chi^2=1.54$, $df=1$, $n=343$, $P=0.22$). Likewise, the survival of offspring in both low and high soil moistures was not dependent on natural variation in brood mass weight (low soil moisture: $\chi^2=1.76$, $df=1$, $n=332$, $P=0.19$; high soil moisture: $\chi^2=1.82$, $df=1$, $n=315$, $P=0.18$). Therefore, for both dung and soil types, once t_{\min} has been exceeded, brood mass weight did not significantly influence offspring survival.

Experiment 4: observed provisioning strategies

To examine the level of provisioning by females on both horse and cow dung, we performed a paired t -test on the mean dry weight and number of brood masses produced on each dung type. Females produced significantly heavier brood masses on cow dung than on horse dung ($t=10.68$, $df=85$, $P<0.0001$), however, they produced significantly fewer of them ($t=2.02$, $df=85$, $P<0.047$) (Table 1). Across individual females, we found a negative association between the number of brood masses produced on cow dung and the number produced on horse dung ($r=-0.254$, $df=85$, $P<0.018$). This association suggests that individual females trade-off increased brood mass weight with reductions in brood mass number when provisioning with cow dung. Furthermore, a trade-off is also evident from the negative correlation between brood mass weight and number, after controlling for body size, within each dung type (horse dung; body size: 0.47 ± 0.06 , $t=7.46$, $df=85$, $P<0.0001$, brood mass number: -0.01 ± 0.007 , $t=2.01$, $df=85$, $P<0.047$; cow dung; body size: 0.76 ± 0.09 , $t=8.92$, $df=85$, $P<0.001$; brood mass number: -0.015 ± 0.005 , $t=2.16$, $df=85$, $P<0.033$).

To examine the level of provisioning by females on both high and low soil moisture, we performed an

Table 1 The mean (\pm SE) dry weight (g) of brood masses and number of brood masses produced by females provisioning with horse dung and cow dung. The sample size is 86 females in each case

	Horse dung	Cow dung
Brood mass weight (g)	2.101 \pm 0.03	2.658 \pm 0.05
Brood mass number	7.132 \pm 0.34	6.034 \pm 0.28

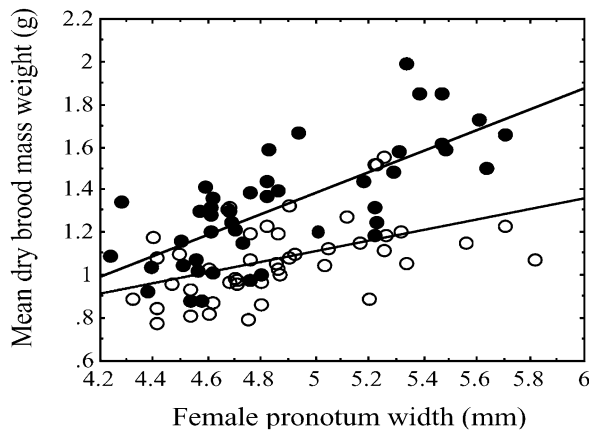


Fig. 3 The relationship between female pronotum width and mean dry brood mass weight for females provisioning on low (*closed symbols*) and high (*open symbols*) moisture soil. The significance of the interaction term indicates a difference of the linear slopes between female size and mean dry brood mass weight for females provisioning on low ($b=0.49\pm0.07$ g/mm, $t=6.82$, $P=0.0001$) and high ($b=0.25\pm0.06$ g/mm, $t=3.62$, $P=0.0007$) soil moisture

Table 2 The mean (\pm SE) dry weight (g) of brood masses and number of brood masses produced by females provisioning with high (10% water content) and low (5% water content) moisture soil. The sample sizes are 47 and 44 females, respectively

	High moisture	Low moisture
Brood mass weight (g)	1.081 \pm 0.03	1.326 \pm 0.04
Brood mass number	12.136 \pm 0.76	12.766 \pm 0.70

ANCOVA with soil moisture as the main effect, female size as the covariate and mean dry brood mass weight and the number of brood masses produced as the dependent variables. There was a significant effect of soil moisture ($F_{(1,89)}=5.02$, $P<0.027$), the covariate female size ($F_{(1,89)}=59.43$, $P<0.0001$), and a significant interaction between the main effect and the covariate ($F_{(1,89)}=7.79$, $P<0.0065$) so that although on average brood masses built in low moisture soil were heavier (Table 2), we must interpret the data at the level of the interaction. Thus, brood masses built by large females were heavier when they provisioned in low moisture soil than in high moisture soil (Fig. 3). In contrast, the number of brood masses produced by a female was only influenced by female size, with larger females producing significantly more brood masses (soil moisture: $F_{(1,89)}=1.76$, $P=0.19$; female size: $F_{(1,89)}=10.15$, $P<0.002$; soil moisture \times female size: $F_{(1,89)}=1.19$, $P=0.17$) (Table 2). After controlling for female body size, there was a significant trade-off between brood mass weight and number on both high (female size: 0.31 ± 0.08 , $t_{46}=4.15$, $P<0.0002$; brood mass number: -0.01 ± 0.006 , $t_{46}=2.04$, $P<0.047$) and low soil moisture content (female size: 0.52 ± 0.07 , $t_{43}=7.44$, $P<0.0001$; brood mass number: -0.01 ± 0.006 , $t_{43}=2.26$, $P<0.03$).

Experiment 5: female preference for dung type

A paired *t*-test between the number of brood masses produced with horse dung and the number produced with cow dung across the 20 replicate populations revealed a significant preference among females for provisioning with horse dung ($t_{19}=11.08$, $P<0.0001$). Females producing approximately three times the number of brood masses on horse dung than on cow dung (horse dung: 35.20 ± 2.74 ; cow dung: 10.35 ± 1.24).

Predicted (t^*) versus observed provisioning times

We predicted the optimal provisioning times for horse and cow dung by substituting the calculated costs ($C=T+t_{\min}$: horse dung, $C=505.33$ min; cow dung, $C=519.07$ min) and rates of fitness gain (horse dung: $r=0.0063$ mm/min; cow dung: $r=0.0058$ mm/min) into equation 2. The error about the predicted optimum was calculated using the mean values of each parameter and the 95% confidence interval. A female's optimal provisioning time was predicted to be greater when provisioning with cow dung ($t^*=299.19\pm2.4$ min) than with horse dung ($t^*=281.43\pm5.34$ min). Theoretically, this is expected given the lower rate of fitness gain (r) and the higher provisioning costs (C) for females provisioning with cow dung (see Fig. 1A). We compared the observed provisioning times of females, taken from the sample of unmanipulated brood masses, to these theoretical optima using a one sample *t*-test. Our predicted optimal provisioning times were significantly lower than the mean observed provisioning times for both cow dung (mean observed= 861.28 ± 7.67 min, $t_{343}=73.33$, $P<0.0001$) and horse dung (mean observed= 736.91 ± 6.67 min, $t_{300}=75.14$, $P<0.0001$).

We also predicted the optimal provisioning times for high and low soil moisture by substituting the calculated costs (low soil moisture: $C=537.30$ min; high soil moisture: $C=336.97$ min) and the rates of fitness gains (low soil moisture: $r=0.0034$ mm/min; high soil moisture: $r=0.0033$ mm/min) into equation 2. A female's optimal provisioning time was predicted to be greater when provisioning on low moisture soil ($t^*=413.82\pm5.12$ min) than on high moisture soil ($t^*=333.99\pm4.98$ min), as expected given the higher provisioning costs (C) (see Fig. 1B). Similarly, our predicted optimal provisioning times were significantly lower than the mean observed provisioning times for both low soil moisture (mean observed= 914.23 ± 8.41 min, $t_{332}=28.12$, $P<0.0001$) and high soil moisture (mean observed= 866.31 ± 7.99 min, $t_{315}=22.16$, $P<0.0001$).

Discussion

Optimal provisioning in a heterogeneous environment

In this study we provide clear evidence that the costs and benefits of maternal investment in the dung beetle

Onthophagus taurus covary with resource quality. Females provisioning with horse dung were shown to receive greater fitness returns per unit of investment and to experience lower provisioning costs, in terms of the minimum amount of dung required to produce a surviving offspring, than females provisioning with cow dung. Accordingly, our theoretically calculated optimal investment levels were considerably lower when females provisioned with horse dung. Moreover, individual females were shown to modify their investment according to dung quality, providing approximately 20% less dung to offspring when provisioning on horse dung. By reducing their investment per offspring and exhibiting a clear preference to provision offspring with horse dung, females were able to produce significantly more offspring.

In contrast, we found that the fitness returns per unit of investment did not vary across habitats of different moisture content. However, we did find that females suffered higher costs when provisioning in low moisture soil. This higher cost was mediated through the construction of longer breeding tunnels, with females provisioning in dryer soil taking over twice as long to produce a breeding tunnel as females provisioning in high moisture soil. Interestingly this cost may be size dependent since we found that, although brood masses were on average heavier in low moisture soil, larger females exhibited a greater response to soil moisture than did small females (Fig. 3). This increased cost predicts a greater investment in brood masses in low moisture soil compared with high moisture soil. Indeed, females were shown to provide relatively greater investment for their body size when provisioning in low moisture soil compared to high moisture soil.

Collectively, the results of this study are in qualitative agreement with marginal value theorem and provide empirical support for the proposal that females can adaptively adjust their level of investment in response to variation in resource quality and both the costs and benefits of provisioning offspring. Furthermore, our findings emphasize the importance that marginal fitness gains will have in determining levels of investment that are provided across heterogeneous environments (Charnov 1976; Lloyd 1987; McGinley et al. 1987; Winkler and Wallin 1987; Stephens and Dunbar 1993).

Quantitative measures of the fitness gains from investment in offspring and the costs of investment to parents have proved difficult to obtain. As such, the majority of empirical studies examining whether parents are able to vary their investment strategies in an adaptive fashion have focussed predominantly on testing qualitative predictions rather than directly quantifying the costs and benefits of investment in offspring (Clutton-Brock 1991; Carrière and Roff 1995; Carrière et al. 1997; Fox et al. 1997). For example, in seed beetles (*Stator limbatus*) larvae developing on the seeds of *Cercidium floridum* are subject to high mortality when penetrating the seed coat, whereas larvae developing on *Acacia greggii* have low mortality (Fox et al. 1997). Consequently, there is strong

selection for laying large eggs on *C. floridum* and small eggs of *A. greggii* (Fox et al. 1997). In a series of controlled laboratory studies, Fox et al. (1997) demonstrated that females laid significantly larger and fewer eggs on *C. floridum* than on *A. greggii* and when switched between hosts, females adaptively readjusted their egg size. However, although providing convincing evidence for egg size plasticity in *S. limbatus*, because Fox et al. (1997) did not quantify the costs and benefits of producing eggs of a given size, their analysis can not determine whether egg size is actually optimised with respect to seed species.

One notable exception providing quantitative measures is the study of clutch size evolution in hymenopteran parasitoids (Godfray 1994). In gregarious species, developing larvae must compete for limited resources during development and offspring fitness is generally inversely related to clutch size (Waage and Ng 1984; Bai and Mackauer 1992; Visser 1994; Iwao and Ohsaki 1996). Direct quantification of the fitness returns for offspring developing at different clutch sizes has shown that the optimal clutch size is strongly influenced by host quality, with smaller clutch sizes being predicted on lower quality hosts that have fewer resources to support larvae (Charnov and Skinner 1984, Godfray 1994). Empirical support for this prediction has been found in numerous species (Waage and Ng 1984; Waage and Godfray 1985; Dijkstra 1986; Takagi 1986; le Masurier 1987; Hardy et al. 1992). However, the majority of studies comparing observed and optimally predicted clutch sizes demonstrate that observed clutch values are typically lower (Waage and Ng 1984; Dijkstra 1986; Taylor 1988; Hardy et al. 1992). One explanation is that the costs associated with locating a suitable host is underestimated and MVT models incorporating these additional costs predict that if the time required to locate and prepare a host are low, optimal clutch sizes will be reduced (Charnov and Skinner 1984, 1985; Iwasa et al. 1984; Parker and Courtney 1984). The exploitation of host cues in many parasitoid species (reviewed by Godfray 1994) may reduce these costs and lower the optimal clutch sizes closer to the observed values.

The applicability of MVT to investment strategies in *O. taurus*

In *O. taurus*, the theoretically predicted optimal investment yielded a poor quantitative fit with our observed levels of investment. Females were shown to provide over twice the investment predicted by the MVT approach. The vast majority of theoretical models examining the evolution of investment strategies have started with two key assumptions: (1) a trade-off between the amount of investment provided to an offspring and a parent's future fecundity and (2) the relationship between offspring fitness and investment per offspring increases monotonically and is asymptotic (Smith and Fretwell 1974; Brockelman 1975; Kaplan and Cooper 1984; Parker and

Begon 1986; Bull 1987; Lloyd 1987; McGinley et al. 1987; García Dorado 1990). Therefore, the success of optimality models in explaining the observed diversity in investment strategies will depend on the validity of these assumptions (and subsequent elaborations) to the specific organism being examined. However, it is unlikely that the assumptions of optimality models will be satisfied in all species, thus questioning the widespread application of MVT to explain the observed diversity of investment strategies (see Bernardo 1996). Below we discuss the validity of the assumptions of MVT to *O. taurus* and how violation of these assumptions and inaccuracies in estimating the costs and fitness returns of investment may generate the disparity between our observed and theoretically derived optimal levels of investment.

A trade-off between per offspring investment and total investment

The MVT approach is based on the premise that the proximate constraint acting on parental investment is resource based. As such, a trade-off between per offspring investment and total investment seems intuitive. In general though, evidence for a trade-off is not conclusive (see reviews by Roff 1992 and Stearns 1992) and numerous examples exist in which such trade-offs do not exist (see Bernardo 1996). In *O. taurus* we found a negative association between the number of brood masses produced on cow dung and the number produced on horse dung. This suggests that females trade-off increased brood mass weight with reductions in brood mass number when provisioning with cow dung. Moreover, when controlling for female size effects, there was a negative relationship between brood mass weight and number in each dung type and soil moisture content. However, unless this trade-off has an underlying genetic basis it will not be of evolutionary significance (Reznick 1985; Roff 1994). In general, the use of phenotypic correlations to measure life history trade-offs has been met with controversy (see Partridge 1992; Reznick 1992) because estimates from phenotypic correlations often differ from those attained through genetic studies (Reznick 1985). Clearly, future studies examining the genetic basis of this phenotypic trade-off in *O. taurus* are required.

The relationship between per offspring investment and offspring fitness shows diminishing returns

In this study we clearly demonstrate that the relationship between per offspring investment and offspring body size shows diminishing returns, with an asymptotic body size being reached where further investment per offspring yields negligible growth advantages (Fig. 2). However, our MVT approach assumes that offspring fitness is directly related to body size as an adult. While this is certainly the case for females (Hunt and Simmons 2000), male fitness increases non-linearly with body size (Hunt

and Simmons 2001). In *O. taurus*, when a sufficient quantity of dung has been provisioned in the brood mass, males develop enlarged horns and adopt a “major” morphology, while offspring receiving below this amount develop as hornless “minor” males (Hunt and Simmons 1997) and must sneak copulations with females that are being guarded by major males (Moczek and Emlen 2000). We have shown that the relationship between fitness and body size is flat across minor males, while male fitness is a positive linear function of body size for major males. Thus, when male offspring are produced, fitness will only increase with investment once enough resources have been provisioned to produce a major male. This additional investment required to produce a major male offspring will thus represent a further cost of investment in sons above t_{\min} .

We can calculate the critical body size required to produced a major son (cow dung=4.30 mm; horse dung=4.65 mm; see Hunt and Simmons 1998b for the application of Eberhard and Gutierrez’s 1991 models for determining the critical switch point in this species). If this is incorporated into equation 2, our total investment costs increase (cow dung: $C=948.93$ min; horse dung: $C=836.75$ min) and subsequent optimal provisioning times also increase (cow dung: $t^*=372.41$ min; horse dung: $t^*=337.94$ min). Since females are unlikely to be able to determine the sex of their offspring, selection for the production of large major male offspring may generally select for the production of larger brood masses. Thus, differences in the shape of the function relating offspring fitness to investment may have important implications for the evolution of investment strategies. Nevertheless, we note that observed provisioning times were still considerably higher than those predicted, even after accounting for this non-linearity in the body size fitness relationship for male offspring.

The only cost of providing investment is T and t_{\min}

In this study we assume that the only costs experienced by a female providing investment is the time required to produce a breeding tunnel and to provision the minimum amount of dung required to produce a surviving offspring. However, the costs of providing investment in *O. taurus* are likely to be far more complex, including such factors as dispersal between dung pads, location of a suitable mate, the maintenance of somatic and gametic reserves for future investment and the survival costs of providing current investment. Therefore, it is clear that our estimates of the costs experienced by females during investment are gross underestimates. Thus, more extensive quantification of the costs associated with providing investment are likely to yield greatly increased costs, raising the theoretically calculated optima closer to the observed values.

All females receive the same fitness returns and costs of providing investment

We assume that all females receive the same fitness returns and experience the same costs when providing investment. By using females at random, our predicted optima are based on the average female in the population and do not account for any differences that may exist in fitness gains and costs between females. However, both theoretical models (Parker and Begon 1986) and empirical studies (Parker and Stuart 1976; Parker and Simmons 1994; Parker et al. 1999) have shown that optimal responses often depend on an individual's phenotype. In the yellow dungfly, *Scatophaga sterocoraria*, large males receive greater fertilization gains during copulation and are more likely to obtain matings through take-overs than are small males (Parker and Simmons 1994). As predicted by marginal value theorem, increased rates of fitness gain and reduced searching costs reduce copula duration, which is typically much shorter for larger males (Parker and Stuart 1976; Parker et al. 1993; Parker and Simmons 1994). Initial analysis of the dungfly system yielded an estimated optimal copula duration that was below the observed (Parker and Stuart 1976). However, including phenotypic effects on fitness gain due to male and female phenotype produced a greatly improved fit (Parker and Simmons 1994, 2000).

In *O. taurus*, the level of investment provided to offspring is strongly influenced by maternal phenotype, with larger females providing greater investment (Hunt and Simmons 2000). If this relationship represents a phenotypic optima, the lack of regard for phenotype in our study may have influenced the fit between observed and expected levels of investment, particularly if female size influences the time to construct a breeding tunnel or the rate at which dung can be deposited into the brood mass. Indeed, this study suggests that the costs of tunneling may be size dependent, since large females had a greater response to low moisture soil than did small females. Clearly, future studies of this species that incorporate the effects of maternal phenotype on optimal investment may prove fruitful.

Concluding remarks

The primary aim of MVT is to generate testable hypotheses and to this end it provides an important tool that has increased our understanding of animal behaviour (Roff 1994). MVT has been applied most extensively to optimal foraging theory, with moderate levels of success (Nonacs 2001). In the majority of cases, foragers show a consistent tendency to reside in a patch for longer than is theoretically predicted (Nonacs 2001). Thus, while there is good qualitative support for MVT predictions, quantitative fits often deviate from prediction (Nonacs 2001). However, this should not be viewed as a deficiency of the MVT approach, rather as a means through which evolutionary studies can progress. We suggest that a more detailed quantification of the fitness gains and costs of providing investment in *O.*

taurus as well as the underlying assumptions of MVT, will undoubtedly improve our understanding of the evolution of maternal investment strategies in this species. Nevertheless, our study provides one of the most detailed accounts of how the costs and benefits of providing care interact to shape parental investment strategies.

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