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Provisioning under the risk of starvation

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ABSTRACT

Providing for altricial young can be risky. Fundamental to understanding the risks involved, along with their management, is the trade-off between current and future reproductive effort. Here we present a dynamic model of provisioning under an important source of risk: starvation. Given the choice of foraging or provisioning at each point in the provisioning period, we show that, when parents have a higher risk of running an energy deficit while foraging, offspring have a poorer chance of surviving to independence. Unexpectedly, our results also predict that, for low to moderate levels of such risk, surviving offspring are likely to show improved condition than if energy intake was more certain; by buffering themselves from the risk of starvation, parents put offspring at risk while ending up with more resources to invest in survivors. As the value of ensuring parental survival decreases, this effect becomes less pronounced and provisioning declines. Thus, a component of reproductive effort can decline with age or increase with longevity in response to a common source of biological risk. These results show that environmental variability can have effects on the evolution of provisioning for altricial young that do not follow from traditional life-history reasoning.

Keywords: central place foraging, dynamic programming, life-history theory, provisioning, starvation risk, stochasticity.

INTRODUCTION

Animals often have to cope with uncertain access to food and significant risks of starving to death. With only finite resources available to an individual, it is crucial to optimize the timing and rate of reproduction with respect to ecological opportunity, especially in a changing world (Partridge and Harvey, 1988; Roff, 1992; Stearns, 1992). Fine-tuning reproductive effort to current conditions by producing relatively cheap, small offspring and provisioning them over a period of dependency is one life-history response shown by a wide range of organisms, from insects to large mammals. These organisms must adjust their investment in current offspring relative to the risks to their own survival and their future prospects for reproduction, if any (Clark and Ydenberg, 1990). Since parents must increase their activity to provide both for themselves and their offspring, they will suffer increased

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risks of mortality. Activity is associated with exposure to predators (Sih, 1987; Lima and Dill, 1990; Lima, 1998) and other environmental dangers; therefore, increasing energetic gain through foraging will often increase the risk of death or injury. In addition, the energetic stress associated with feeding young can also increase the chance that parental energy reserves will fall below levels necessary for their own sustenance, particularly when foraging returns are variable. This risk of starvation may be particularly influential to provisioning decisions, since parents must survive until the young can fend for themselves to gain any fitness payoff from even the current reproductive attempt. The risk to parenting from predation has received the bulk of attention in the literature (e.g. Clark and Ydenberg, 1990; Magnhagen, 1991, 1992; Harfenist and Ydenberg, 1995; Lima, 1998; Martin *et al.*, 2000), while how the risk of parental starvation is managed is less well understood.

The notion of trading off energy for self-maintenance against offspring growth and survival is reminiscent of the central tenet of life-history theory: investment in the current reproductive attempt can reduce the capability for future reproduction (Partridge and Harvey, 1988; Roff, 1992; Stearns, 1992). Indeed, the reproductive value of parental survival relative to the value of offspring state at the end of the provisioning period can be used to relate the consequences of provisioning decisions to this important life-history trade-off. Moreover, how environmental variability affects life-history strategies is receiving an increasing amount of attention from researchers (e.g. Benton and Grant, 1999; Brommer *et al.*, 2000). Here we deviate from such approaches by focusing on the dynamics of energy reserve management by parents in the face of environmental uncertainty. This focus, using dynamic state variable models, has proven very successful in understanding the trade-offs involved with energy reserve management in general, including under the influence of food supply, metabolic costs, predation risk and social interactions (for reviews, see Houston and McNamara, 1999; Clark and Mangel, 2000), and is proving invaluable for analysing the effects of fine-grained environmental stochasticity on life-history strategies (Houston and McNamara, 1999; Tenhumberg *et al.*, 2000). Moreover, such models have been proposed in the context of caring for altricial young (Beauchamp *et al.*, 1991; Winkler and Adler, 1996; Welham and Beauchamp, 1997). However, while these previous treatments of parental care focused on state-dependent behavioural dynamics in a particular system (Beauchamp *et al.*, 1991) and the relative performance of different provisioning currencies (Welham and Beauchamp, 1997), we investigate the trade-off between parental and offspring state under energetic risk in general, and how it is influenced by residual reproductive value. Thus, our treatment is a fine-scale investigation of the consequences of an important source of demographic stochasticity for income breeders (Houston and McNamara, 1999; Stearns, 1992). As such, it adds mechanistic detail to the typically coarse-grained approach adopted by life-history theory, as well as expanding the scope of existing theories of central place foraging and provisioning (Stephens and Krebs, 1986; Houston, 1987; Clark and Ydenberg, 1990; Beauchamp *et al.*, 1991; Welham and Beauchamp, 1997).

We develop a dynamic optimization model of provisioning under the risk of energetic shortfall while foraging. We assume that the decision to breed has already been made. Hence, our focus is on parental behaviour throughout the period when current altricial young are totally dependent: post-natal or hatching, until weaning or fledging. For simplicity, we do not consider any conflict between parents, or with the offspring. Indeed, we assume that a single parent provisions the brood, which is considered unitary (i.e. can be represented by a single state variable). In addition, we assume that all of the parental reserves are available for provisioning, if the parent so chooses (a potential output from our

model). We find the policy that maximizes an animal's fitness as a function of its state, and that of its offspring, at the end of a provisioning period. Our goal is to characterize the effects of energetic risk on provisioning effort, and the consequent mortality rates of parents and current offspring, under a broad range of conditions. We model energetic risk as stochasticity in foraging returns (independent of the mean), or, specifically, the probability of an energetic shortfall while foraging.

THE MODEL

Terms and their baseline values are defined in Table 1. A detailed specification is given in the Appendix. Behaviour is modelled as a sequence of decisions made at times $t = 1, 2, \ldots$ An animal is characterized by the state of its energetic reserves at t, $X(t) = x$, along with the equivalent state of its offspring's reserves, $Y(t) = y$. If, at any point, either of these variables drops to its critical value, X_{crit} or Y_{crit} respectively, the parent or offspring is assumed to have died from starvation. Similarly, the state variables cannot exceed X_{max} or Y_{max}, which represent the maximum reserves that the parent or offspring can maintain. We assume that the parent behaves so as to maximize its fitness F at T, the end of the provisioning period. Specifically, the terminal fitness function is the sum of payoffs from the parent's own state and that of its offspring:

$$F(x,y,T) = \gamma(x) + \theta(y) \tag{1a}$$

where

$$\gamma(x) = \begin{cases} 0, & x \le X_{crit} \\ \Phi, & X_{crit} < x \le X_{max} \end{cases} \tag{1b}$$

and

$$\theta(y) = \begin{cases} 0, & y \le Y_{crit} \\ \Omega \dfrac{y - Y_{crit}}{y - Y_{crit} + y_0}, & Y_{crit} < y \le Y_{max} \end{cases} \tag{1c}$$

Φ is the payoff to the parent for being alive at T and is, therefore, a measure of expected future reproduction ($\equiv R$; Clark and Ydenberg, 1990). We assume that this will be insensitive to the state of parental energy reserves at the end of the provisioning period, since adults should regain condition rapidly once the stress associated with provisioning is alleviated. Such an assumption follows from our focus on post-reproductive investment decisions, which may affect the classic life-history trade-off between current and future reproductive effort only indirectly. As is evident from (1c), we assume that the payoff from a successful breeding attempt is an increasing, if decelerating, function of offspring state at T. Ω is the limit $y \to \infty$ of this function, thus representing the maximum possible fitness value of producing independent offspring under current conditions, with y_0 a constant specifying the steepness of the increase in θ with y: specifically, $\theta(y) = \frac{1}{2}\Omega$ when $y = Y_{crit} + y_0$ (Clark and Mangel, 2000). In this way, we model the very general case in which body condition at independence has significant consequences for lifetime reproductive success (e.g. Hall *et al.*, 2001).

At each t (e.g. the beginning of each day), a parent can decide whether to forage or provision. If it decides to forage, we assume that the animal will find food of expected energetic value e with probability p in a time period, and no food otherwise $(1 - p)$. In

Table 1. Provisioning under energetic risk

Term and baseline value	Definition
$T = 60$	length of provisioning period
t	unit of time at which behavioural decisions are made (e.g. a day)
$X(t) = x$	state of energy reserves of the parent at t
$Y(t) = y$	state of energy reserves of the offspring at t
$\gamma(x)$	payoff to parent at T as a function of x (see (1b))
$\theta(y)$	payoff to parent at T as a function of y (see (1c))
$y_0 = 25$	constant determining steepness of increase in θ with y (1c)
X_{crit}, $Y_{crit} = 0$	levels of reserves at which starvation occurs
$X_{max} = 100$, $Y_{max} = 20$	maximum reserves that can be stored
$X_{init} = 80$, $Y_{init} = 20$	initial states for computation of expected optimal behaviour
e	net energy gained per food encounter
p	probability of encountering food each time step
$\mu = p \cdot e = 15$	mean amount of food obtainable per time step when foraging
$\pi = 5$	amount of energy provisioned per time step
$\varepsilon(t)$	proportion of π that is converted to offspring reserves as a function of t (see (2))
$\varepsilon_0 = 0.97$	initial value of ε()
$k = 1.333$	constant determining magnitude of $\varepsilon(T)$ (see (2))
$C_f = 10$	metabolic cost to parent of being out foraging per unit time
$C_p = 5$	metabolic cost to parent of remaining to provision per unit time
$C_o = 2$	metabolic cost to offspring per unit time

addition, it will incur an energetic cost C_f per time step. On the other hand, if the parent decides to provision, it will suffer a metabolic cost C_p, in addition to providing energy to its offspring from its reserves at a rate of π per time step, should the offspring be alive at t. However, not all of this energy will be converted into offspring reserves; some will also be allocated to growth. Therefore, we assume that, while the parent is provisioning, offspring reserves will be incremented by some proportion ε of π per unit time. Moreover, we assume that ε is a decreasing function of t; the larger the offspring becomes, the more energetically demanding growth becomes (Winkler and Adler, 1996), and hence an increasingly smaller proportion of π is converted into offspring reserves over time. Specifically,

$$\varepsilon(t) = \varepsilon_0 - \frac{\varepsilon_0 t^2}{(kT)^2} \tag{2}$$

where ε_0 is the proportion of π that is converted to offspring reserves at the start of provisioning, and k is a constant that specifies the magnitude of ε at T; that is, $\varepsilon(T) = \varepsilon_0 - (\varepsilon_0/k^2)$. Throughout, we assume that foraging is more energetically costly than remaining with the offspring to provision (independent of the actual energy provisioned); in other words, $C_f > C_p$. Regardless of what the parent does, offspring will incur a metabolic cost C_o per time step. For simplicity, all metabolic costs are assumed to be independent of state. The resultant state dynamics are detailed in the Appendix.

We find the strategy that maximizes the parent's fitness at T, specified by (1). A strategy is a rule for choosing between the actions available to a parent during the provisioning period based on its state and that of its offspring. Since the fitness consequences of an

action depend on future actions, we solve for the optimal strategy numerically, using dynamic programming (Houston *et al.*, 1988; Mangel and Clark, 1988). The dynamic programming equations are also given in the Appendix.

RESULTS

To understand the implications for expected behaviour of the optimal strategy, determined by dynamic programming, we calculated the likelihood that parents following the optimal strategy would be in a particular state, or subset of states (and hence behaving in a particular way), at each decision point in the provisioning period after specifying initial states, X_{init} and Y_{init} (Houston and McNamara, 1999). We express all results as the proportion of time spent in a given state (for mortality rates and state values) or performing a particular action, as computed directly in this way.

Our main result is that, as the risk of energetic shortfall when foraging increases (increasing $1 - p$, holding all else constant, including mean foraging returns, μ), the proportion of offspring surviving the provisioning period declines, but those that survive show better condition than when energy intake is more certain. The latter effect holds for low to moderate risk; beyond a certain probability of not finding food, final offspring state declines with increased risk, in step with the probability of surviving to independence. This result is very general to our formalization; it holds for a wide range of parameter values providing certain basic conditions hold. First, there must be a non-zero probability that offspring will survive to T. In addition, the provisioning period must be long enough, and the energetic trade-offs associated with the various activities such, that parental and offspring survival are not trivial concerns. To understand why we get this effect of risk, we begin by considering the case in which all fitness accrues from the current breeding attempt: $\Phi = 0$. Figure 1 illustrates the qualitative result described above under these conditions.

An important effect of reducing the chance of finding food while foraging is that it will increase the amount of time that the parent should commit to foraging when there is a substantial amount of time left until T. This is because increased uncertainty in intake will select for the maintenance of reserves as a buffer against starvation (Houston *et al.*, 1993; Houston and McNamara, 1999), which requires foraging effort. It follows then, in our model, that provisioning of offspring will decline in such circumstances. This is illustrated in Fig. 2; the proportion of time spent provisioning decreases with the probability of finding food when foraging early and in the middle of the provisioning period. Devoting time to foraging at these times will minimize the risk of parental starvation and sacrificing *any* chance of a payoff; offspring are totally dependent on the parent until they can survive until T on their own $[t \geq T - (y/C_o)]$. However, this will be achieved at the cost of increasing the chance that the offspring will die of starvation in the meantime; although this is less than certainty, thus offering a non-zero expected payoff when $\Phi = 0$. It is for this reason that the proportion of offspring surviving until independence declines with the probability of finding food (Fig. 1).

The maintenance of a buffer against starvation risk discussed above will result in the parent being in a better state upon entering the final phase of its provisioning period as the certainty of intake declines. Figure 3 shows that the parent will defend a higher state for longer as p declines, to minimize its risk of starving before its offspring can get by on its/their own. The better the condition the parent is in as it enters the phase when provisioning

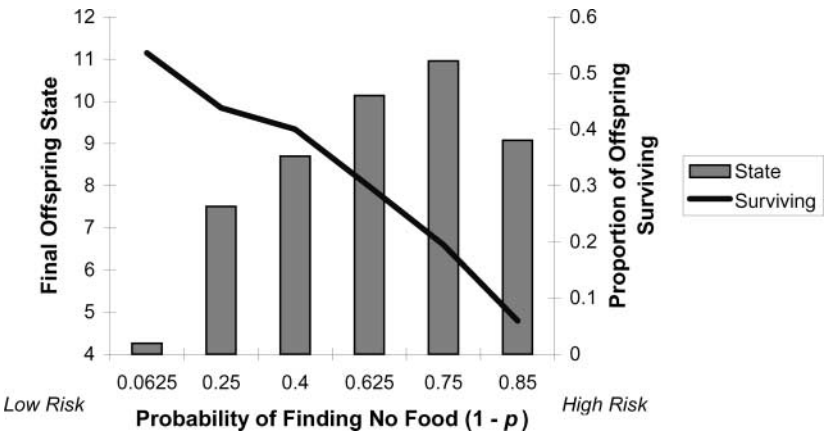

Fig. 1. The results of the dynamic optimization model (see text) showing the effects of varying the probability of finding food, p, and its expected value, e, to manipulate the risk of an energetic shortfall when foraging while holding mean returns, $\mu = 15$, constant. Plotted are the state and proportion of offspring surviving at the end of the provisioning period, T. Here all fitness accrues from the current breeding attempt: $\Phi = 0$ ($\Omega = 50$); the values of the other parameters are given in Table 1.

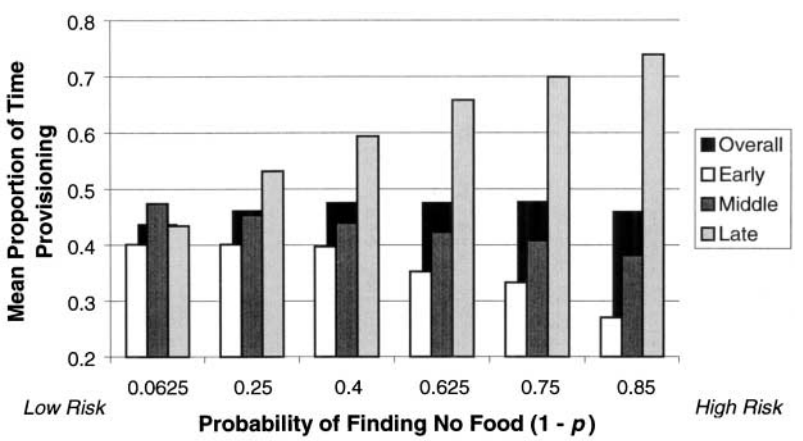

Fig. 2. The results of varying the risk of an energetic shortfall (p and e holding $\mu = 15$; as in Fig. 1) on the mean proportion of time the parent should spend provisioning early ($0 < t \leq T/3$), in the middle ($T/3 < t \leq \frac{2}{3}T$) and late ($\frac{2}{3}T < t < T$) in the provisioning period. Here all fitness accrues from the current breeding attempt: $\Phi = 0$ ($\Omega = 50$); the values of the other parameters are given in Table 1.

effort will have a significant effect on final offspring state [$t \geq T - (y/C_o)$], the more provisioning it should do (Fig. 2), and the higher the final offspring state will be (Fig. 3). However, if the risk of an energetic shortfall is such that the level of reserves defended to buffer against parental starvation is forced down, final offspring state will also decline (Fig. 1). The level of parental reserves that can be defended is determined by two factors. First, the amount of energy a parent is able to store is determined by the amount of foraging it can do; to defend a given level of reserves, the proportion of time spent foraging must increase as p declines,

all else being equal (Houston *et al.*, 1993; Houston and McNamara, 1999). In addition, however, there is a minimum amount of provisioning necessary to gain returns from the current breeding attempt; in other words, there should be enough provisioning throughout to guarantee a non-zero probability of offspring survival, particularly when $\Phi = 0$. Therefore, once time spent foraging is constrained by the risk of losing the offspring, the level of reserves maintained must decline as uncertainty of intake increases, since access to food is becoming increasingly restricted.

Increasing the value of future reproduction relative to the current effort exacerbates the qualitative effect of decreasing the probability of finding food in our model. This is achieved by varying $\Phi/(\theta(Y_{max}))$ in Fig. 4; decreasing p decreases the proportion of offspring surviving and increases the mean state of surviving offspring more as this fraction increases, especially at the moderate levels of risk where this effect is most pronounced ($p \approx 0.35$). This is because, as the relative value of parental survival increases, so does the level of parental reserves that should be maintained, at the expense of provisioning and therefore the risk of offspring starvation (Fig. 4). This is illustrated in Fig. 5. However, the higher level of parental reserves that is defended will allow more provisioning effort by those parents whose offspring are alive in the terminal phase of provisioning. Indeed, the level of provisioning in the final phase can become so high that it actually increases the mean level of provisioning over the whole period of dependency (Fig. 6). Therefore, if provisioning effort were to be estimated in such a crude way, observers might draw the counter-intuitive conclusion that individuals with the most future reproductive potential (e.g. younger ones, or long-lived species) invest relatively more effort in each breeding attempt!

DISCUSSION

We focus here exclusively on provisioning by single parents, assuming that a parent acts to maximize its fitness at the end of the period of dependency; future reproductive payoffs accrue if the parent survives, while the value of the current breeding attempt depends on final offspring reserves. Given a periodic choice of foraging or provisioning, we show that, when parents run a higher risk of energy deficit while foraging, offspring have a lower chance of surviving to independence. This result concurs with conventional life-history theory expectations (Roff, 1992; Stearns, 1992), and the predictions from previous state-dependent models of parental care as environmental conditions deteriorate (Beauchamp *et al.*, 1991; Welham and Beauchamp, 1997). However, unexpectedly from such perspectives, our results also suggest that the surviving offspring will be in better condition than if energy intake was more certain, for low to moderate risk (Fig. 1). This is because the amount of foraging required for parental survival increases as foraging success becomes more uncertain, especially early on. Consequently, under increased energetic risk, provisioning will be reduced early on (Fig. 2) and high levels of parental reserves defended until just before weaning or fledging (Fig. 3). The latter effect is in accordance with predictions about dynamic reserve management under a wide range of circumstances (e.g. Houston *et al.*, 1993; Clark and Ekman, 1995; Brodin and Clark, 1997). This will increase offspring mortality rates, but leave parents with more energy to commit to the final reserves of surviving offspring. This effect is exacerbated by increases in the value of the future, due to higher premiums on parental survival (Figs 4–6). At very high levels of energetic risk, however, it becomes impossible to defend the parental reserves required for high levels of late-phase investment in surviving offspring. Both

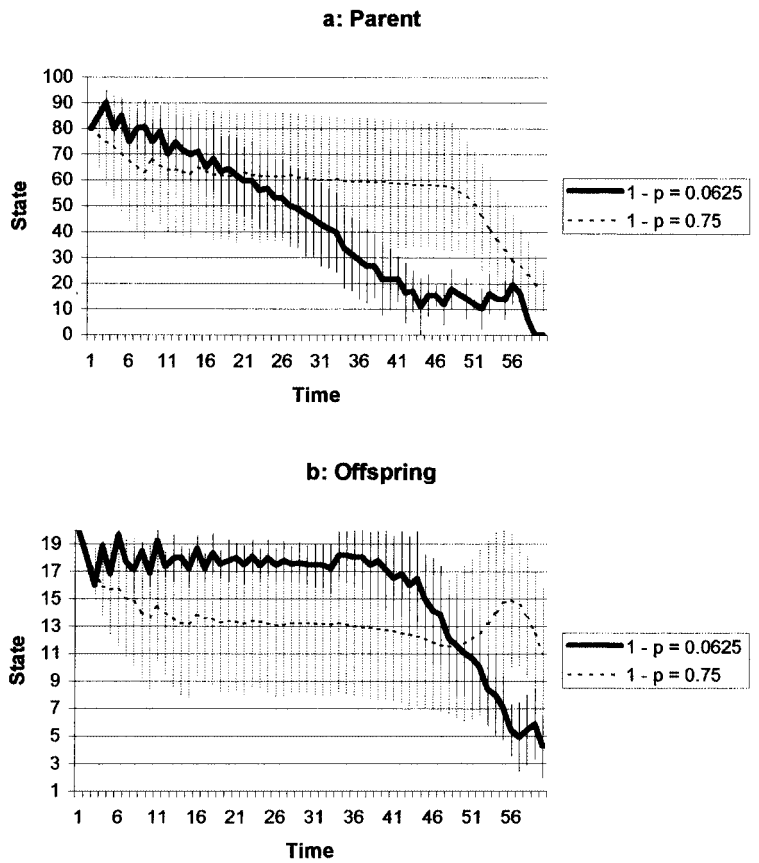

Fig. 3. Each plot is a run of the model showing how the mean states (± 1 standard deviation) of the parent and offspring change over the provisioning period, varying the risk of an energetic shortfall (p and e holding $\mu = 15$ constant). Here all fitness accrues from the current breeding attempt: $\Phi = 0$ ($\Omega = 50$); the values of the other parameters are given in Table 1. (a) Parental state trajectories and (b) offspring state trajectories for $1 - p = 0.0625$ and 0.75, and $e = 16$ and 60, respectively.

offspring survival and final condition fall as risk increases under such circumstances (Figs 1 and 4).

Since our aim was to determine how the risk of parental starvation during the period of offspring dependency affects post-reproduction investment decisions in general, our treatment has been necessarily schematic. Indeed, to maximize analytical clarity by attempting the simplest possible model, we have glossed-over a number of biological realisms, which may also be significant. We address a couple here.

At the heart of our formulation is the assumption that the energetic costs of choosing an action are independent of what the parent is doing. In other words, we assume that there are no additional costs associated with switching actions rather than continuing to forage or provision. This could restrict the potential applicability of our results. For instance, where the parent must range widely to find food – and, therefore, remaining (out or in) versus switching becomes a meaningful distinction – one might expect less behavioural flexibility

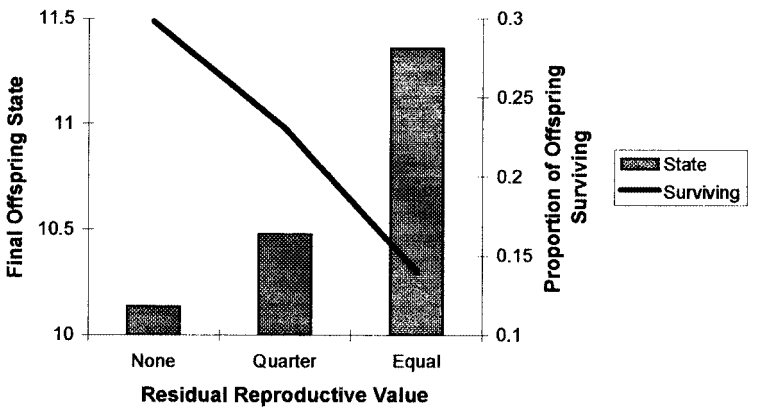

Fig. 4. The results of runs of the model varying the relative value of future reproduction (residual reproductive value). Throughout: the probability of not finding food, $1 - p$, = 0.625 ($e = 40$), $\Omega = 50$, None = all fitness accrues from the current breeding attempt ($\Phi = 0$), Quarter = the future is worth a quarter of the best current breeding attempt [$\Phi/(\theta(Y_{max})) = \frac{1}{4}$], Equal = the future is equally as valuable as the best current attempt [$\Phi/(\theta(Y_{max})) = 1$]; the values of the other parameters are given in Table 1.

than our model predicts. We expect switching costs to exacerbate the qualitative result we describe; parents should be less inclined to 'pop back' to provision when the onus is on minimizing their risk of starvation, and to 'nip out' to forage when final offspring state becomes important. Hence, the qualitative change in behaviour over the provisioning period, and its consequences, are likely to become more pronounced.

On the other hand, it is not possible to generalize our results directly to circumstances in which the parent must decide how much to provision while foraging. This is the case where not all parental reserves are available for provisioning (e.g. in regurgitation provisioners). It is possible that this type of provisioning will have little effect on our results, since parents are still free to 'top up' their own reserves whenever they need to (either from income or the potential investment 'set aside' for their offspring) and thereby manage their risk of starvation in a similar way. Alternatively, having to make provisioning decisions before current income has been tallied may restrict the flexibility of investment necessary to get the results we obtain here. Further work is required to understand the consequences of this mode of provisioning for managing the risk of parental starvation during offspring dependency (e.g. analyse the decision in terms of how much of the foraging returns to allocate to self versus offspring per decision step; Beauchamp *et al.*, 1991; Welham and Beauchamp, 1997).

In contrast to the predicted influence of other sources of risk to parenting (e.g. Clark and Ydenberg, 1990), our results suggest that overall investment in the current brood can go up as the risk of starving increases, under some circumstances. On the other hand, our model also predicts an increase in investment under risk with brood age, which is in line with other work based on parental investment theory (Coleman and Gross, 1991; Magnhagen, 1992; Lavery, 1995; Galeotti *et al.*, 2000). Such relationships illustrate the complexities involved with managing different types of risk in the context of provisioning altricial young. Moreover, within a life-history context, our findings suggest further subtlety in the effects of environmental variability. On the one hand, the general effect of energetic risk we predict

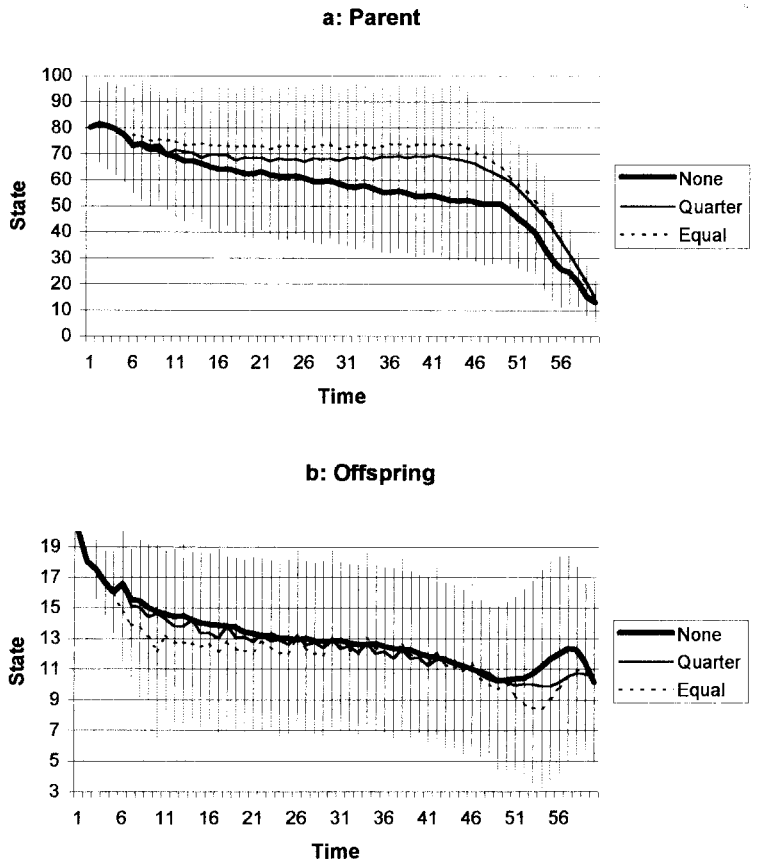

Fig. 5. Each plot is a run of the model showing how the mean states (± 1 standard deviation) of the parent and offspring change over the provisioning period. Throughout: the probability of not finding food, $1 - p, = 0.625$ ($e = 40$), $\Omega = 50$; the values of the other parameters are given in Table 1. (a) Parental state trajectories and (b) offspring state trajectories for different residual reproductive values. None = all fitness accrues from the current breeding attempt ($\Phi = 0$), Quarter = the future is worth a quarter of the best current breeding attempt [$\Phi/(\theta(Y_{max})) = \frac{1}{4}$], Equal = the future is equally as valuable as the best current attempt [$\Phi/(\theta(Y_{max})) = 1$].

here (Figs 1 and 2) is in broad agreement with recent findings on the influence of environmental variability on life-history strategies; where adult and juvenile survivorships are positively related (as they are here), increased variability tends to increase the optimal level of reproductive effort to maximize reproductive output, particularly in bad years (Benton and Grant, 1999). However, by focusing solely on variability within a season, we show that this effect can be non-linear, with maximal reproductive effort (provisioning) predicted at intermediate levels of variability (Figs 2 and 6). On the other hand, conventional wisdom predicts an increase in reproductive effort with reduced residual reproductive value (increased age or shorter lifespans) under most conditions (Roff, 1992). In contrast, our analysis suggests that a component of reproductive effort, provisioning, is predicted to

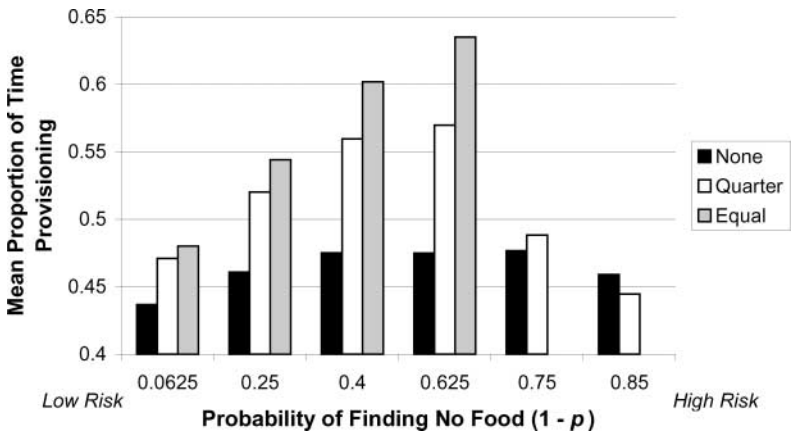

Fig. 6. The results from varying the risk of an energetic shortfall (p and e holding $\mu = 15$; as in Fig. 1) on the mean proportion of time spent provisioning over the whole period when the relative value of the future is varied. Throughout: $\Omega = 50$, None = all fitness accrues from the current breeding attempt ($\Phi = 0$), Quarter = the future is worth a quarter of the best current breeding attempt [$\Phi/(\theta(Y_{\max})) = \frac{1}{4}$], Equal = the future is equally as valuable as the best current attempt [$\Phi/(\theta(Y_{\max})) = 1$]; the values of the other parameters are given in Table 1.

covary *positively* with residual reproductive value, under a common source of demographic stochasticity (Houston and McNamara, 1999).

Our findings may also have some empirical importance. Among marine predators such as seabirds and seals, there is a clear separation between the location of the offspring (on land) and the location of feeding (at sea). There has also long been interest in using the behaviour of these species as indictors of marine food supplies (Cairns, 1987; Monaghan, 1996). However, the complexity of the response of these species to changes in food distribution or abundance has been difficult to interpret in simple terms (Boyd, 1999). The present study provides a framework within which to interpret changes in behaviour associated with changing resource levels. Since resource levels and uncertainty are probably highly correlated, in a practical sense it may not be possible to disentangle the two types of variability. The general observation among these species is that the proportion of time spent provisioning offspring declines as resources decline (Monaghan, 1996; Boyd, 1999). Our model suggests that this can be driven primarily by increased variance in foraging returns irrespective of mean resources, at least for the first half of the period in which offspring are reared (Fig. 2). Moreover, there are several predictions of this model that can be tested experimentally to verify how influential such variability is. Specifically, the predictions that, when faced with increased uncertainty, parents will tend to defend their body reserves to the detriment of their offspring, and also that increasing uncertainty leads to greater disparity in behaviour between different stages of the period in which offspring are reared. For the former prediction, circumstantial evidence comes from recent observations that, in Galapagos fur seals, mothers store more fat to the detriment of pup survival in years of low productivity (Trillmich and Kooyman, 2001).

In conclusion, by attempting the simplest possible model of provisioning under the risk of parental starvation, we have shown that variance in foraging returns can have profound

consequences for seasonal patterns of investment in, and the success of, the current breeding attempt. In the process, we hope that our fine-scale analysis will add to existing life-history theory by illustrating a mechanism by which variability can influence the evolution of a common life-history strategy, provisioning for altricial young.

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APPENDIX: DETAILED SPECIFICATION OF THE MODEL

State transitions

At each $t = 1, 2, \ldots, T$, suppose an animal, characterized by the state of its energetic reserves $X(t) = x$ and that of its offspring $Y(t) = y$, can choose between two actions: u_1 = 'forage' or u_2 = 'provision'. Note that $X_{\text{crit}} < x \leq X_{\max}$ and $Y_{\text{crit}} < y \leq Y_{\max}$ (Table 1); if $x \leq X_{\text{crit}}$ the parent starves, and if $y \leq Y_{\text{crit}}$ the offspring dies of starvation.

Foraging

If it chooses u_1, it consumes food of expected energetic value e with probability p and nothing with probability $1 - p$. Therefore, its potential state transitions are

$$x_1' = x + e - C_{\text{f}} \tag{A1a}$$

and

$$x_1'' = x - C_{\text{f}} \tag{A1b}$$

respectively, where C_f is the metabolic cost of foraging between t and $t + 1$. In addition, its offspring's state transition is always

$$y_1' = y - C_o \tag{A2}$$

with C_o being the metabolic cost to the offspring over the time period.

Provisioning

Alternatively, if the parent chooses u_2, it suffers a metabolic cost $C_p < C_f$, and can provide π units of energy to the offspring from t to $t + 1$. Therefore, so long as $y > Y_{crit}$,

$$x_2' = x - \pi - C_p \tag{A3a}$$

Otherwise, if $y \leq Y_{crit}$,

$$x_2'' = x - C_p \tag{A3b}$$

Equivalently, its offspring's state transitions are

$$y_2' = y + \varepsilon(t) \cdot \pi - C_o \tag{A4a}$$

and

$$y_2'' = Y_{crit} \tag{A4b}$$

respectively, where $\varepsilon(t)$ is the proportion of π that is transformed into offspring reserves defined in (2).

Dynamic programming equations

Let $F(x, y, T)$, defined in (1), be the fitness of the parent at T. Similarly, $F(x, y, t)$ is its fitness at $t = 1, \ldots, T - 1$. Following (A1) – (A4), set

$$V_1(x, y, t) = p \cdot F(x_1', y_1', t, +1) + (1 - p) \cdot F(x_1'', y_1', t + 1) \tag{A5}$$

and

$$V_2(x, y, t) = F(x_2', y_2', t + 1) \tag{A6a}$$

if $y > Y_{crit}$, or

$$V_2(x, y, t) = F(x_2'', y_2'', t + 1) \tag{A6b}$$

otherwise. The optimal action $u^*(x, y, t)$ for the parent is then the value of i that maximizes $F(x, y, t; i)$. That is,

$$F(x, y, t; u^*(x, y, t)) = \max_{i=1,2} V_i(x, y, t) \tag{A7}$$

and

$$F(x, y, t) = \max_{i=1,2} V_i(x, y, t) \tag{A8}$$