

Evolution of mammals: lactation helps mothers to cope with unreliable food supplies

Sasha R. X. Dall^{1†*} and Ian L. Boyd^{2‡}

¹*Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK*

²*Sea Mammal Research Unit, Gatty Marine Laboratory, University of St Andrews, St Andrews KY16 8LB, UK*

Lactation is a ubiquitous feature of mammalian reproduction. Because lactating females can draw on their nutrient reserves for milk production, it offers mothers and their dependent young independence from fluctuations in their food supplies. However, converting food to reserves and milk is relatively inefficient at delivering nutrients to offspring. We use dynamic programming to contrast the performance of mothers that provision dependent, refuge-bound offspring optimally from their nutrient reserves with otherwise equivalent mothers that do so directly from the food they find. In this way, we demonstrate formally that the selective advantage to lactating mothers, who can provision—at a cost—without having found food recently, can be substantial with uncertain food supplies and few opportunities for future reproduction under a wide range of circumstances. Hence, it is likely that unreliability associated with the lifestyles of the small, primitive mammal-like reptiles that evolved extended maternal care, selected for fully-developed milk production and consumption, prompting the evolution of true mammals. Moreover, this work suggests that selection for coping with unreliable food access during provisioning may underlie key life-history differences between birds and mammals because the mass constraints imposed by flight restrict the level of reserves that mothers can carry and provision from.

Keywords: lactation; provisioning; starvation risk; dynamic programming; central place foraging; evolution of mammals

1. INTRODUCTION

Lactation characterizes mammals, and understanding its origins is fundamental to elucidating mammalian evolution. Moreover, the adoption of lactation as a mode of feeding young is thought to be related directly to the evolution of many other mammalian traits (Pond 1977, 1998; Hayssen *et al.* 1985; Blackburn *et al.* 1989; Hayssen 1993). However, since Darwin, the evolution of lactation has troubled evolutionary biologists. It is a ‘complex adaptation’ with highly integrated components, including the morphological, physiological and behavioural aspects of milk production, ingestion and digestion (Blackburn *et al.* 1989; Hayssen 1993). Indeed, early critics of Darwin’s thesis targeted lactation as a problem for gradualist explanations (Mivart 1871), and the incipient stages in the evolution of milk production remain particularly difficult to explain (Blackburn *et al.* 1989). Accordingly, the selection pressures favouring the evolution of lactation remain unresolved. Here we explore formally, for the first time to our knowledge, a fundamental trade-off associated with feeding milk to dependent young with unreliable food supplies in a context that is relevant to the evolutionary origins of lactation.

Animals often face uncertain access to food, which can be particularly challenging for parents feeding young given the high metabolic demands of growth and relative sensitivity of offspring to environmental conditions (Dall & Boyd

2002). The production of nutritious secretions by the mother offers reliable nourishment to offspring and is a universal feature of mammalian reproduction. Indeed, because lactating females can draw on their nutrient reserves for milk production (Pond 1998), lactation offers mothers and their dependent young independence from fluctuations in their food supplies (Pond 1977, 1984). However, producing such nutritious secretions is also associated with substantial inefficiencies compared with the alternative of delivering food to young directly; it takes time to convert nutrients from food to milk, and biochemical reactions are never 100% efficient and so energy, at the very least, will be wasted. To explore systematically how important this trade-off can be, we model the optimal provisioning decisions of income breeders (Stearns 1992) with altricial young at a central place (a refuge, e.g. a nest or burrow) and unreliable food supplies. In fact, the direct ancestors of mammals are thought to be small insectivores (Luo *et al.* 2002) and some species may have sheltered in burrows (Groenewald *et al.* 2001). We contrast the best possible performance of (otherwise equivalent) mothers who provision directly from the food they find (a form of parental feeding presumed to be ancestral, and common in birds) with those who provision—produce milk—from their nutrient reserves, which can include nutrients circulating in the blood stream (Pond 1998). In this way, we present the first rigorous exploration, to our knowledge, of relative adaptive value of ‘provisioning with specialized products or secretions’ (Clutton-Brock 1991) under uncertain access to food, which will provide insights

* Author for correspondence (sashadall@iname.com).

† Address from January 2005: Centre for Ecology and Conservation, University of Exeter in Cornwall, Tremough Campus, Penryn TR10 9EZ, UK.

Table 1. ‘Regurgitation’ and ‘lactation’ 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
$\Phi = 0$	pay-off to parent of being alive at T (residual reproductive value: see equation (2.1b))
$\theta(y)$	pay-off to parent at T as a function of y (see equation (2.1c))
$y_0 = 25, \Omega = 50$	constant determining steepness of increase in θ with y (equation (2.1c)); limit of this function (maximum possible value of producing offspring under current conditions)
$X_{\text{crit}}, Y_{\text{crit}} = 0$	levels of reserves at which starvation occurs
$X_{\text{max}} = 100, Y_{\text{max}} = 20$	maximum levels of reserves that can be stored
$X_{\text{init}} = 80, Y_{\text{init}} = 20$	initial states for computation of expected optimal behaviour
e	net energy gained per food encounter
p	probability of encountering food in each time-step
$\mu = p \times e = 20$	mean amount of food obtainable per time-step when foraging
$\pi = 5$	amount of energy provisioned per time-step
$r = e - \pi$	remaining food available for parental consumption after setting π aside
$\varepsilon(t)$	proportion of π that is converted to offspring reserves as a function of t (see equation (2.2))
$\varepsilon_R = 0.97, \varepsilon_L = 0.9$	initial value of $\varepsilon()$ for regurgitation, lactation respectively
$k = 1.333$	constant determining magnitude of $\varepsilon(T)$ (see equation (2.2))
$CR_f, CL_f = 10$	metabolic cost to parent of foraging (searching = 5 + consuming/continuing to search = 5) per unit time for regurgitation, lactation respectively
$CR_p = 18, CL_p = 5$	metabolic cost to parent of provisioning per unit time for regurgitation: locating food (= 5) + provisioning to central place (round-trip travel = 10 + food delivery = 3); lactation: remaining at central place
$C_s = 5$	metabolic cost of switching activities (travel to or from central place)
$C_o = 2$	metabolic cost to offspring per unit time

into the conditions favouring the evolution of lactation and milk consumption in the mammalian lineage.

Because the allocation of effort to provisioning will depend both on the length of offspring dependency and maternal and offspring condition, which will vary over time, we develop dynamic optimization models of ‘regurgitation’ (provisioning directly from located food) and ‘lactation’ (provisioning from maternal nutrient reserves). We restrict our attention to energy given its convenience for relating the short-term consequences of behaviour to fitness where nutrition is concerned (Stephens & Krebs 1986), and because the logic of our analysis holds for any limiting nutrient obtained from food. 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: postnatal or hatching, until weaning or fledging. For simplicity, we do not consider any conflict between parents, or with the offspring. Indeed, we assume, as is likely in taxa with parental feeding and internal fertilization, that a single mother provisions the brood, which is considered unitary (i.e. can be represented by a single state variable). Throughout, we also assume that offspring are much more sensitive to variation in the time between feeding events than the parent; they can store fewer reserves and their metabolic demands use up a greater proportion of energetic input, which increases as they grow. Using dynamic programming (Houston *et al.* 1988; Mangel & Clark 1988), we find the policies that maximize the mothers’ expected fitness as a function of their state, and that of their offspring, at the end of a provisioning period. We contrast the effects of energetic risk on optimal provisioning effort under regurgitation and lactation, and the consequent mortality rates of offspring

(and mothers), along with their condition at independence. We model energetic risk as stochasticity in foraging returns, or, specifically, the probability of an energetic shortfall while foraging (Dall & Boyd 2002).

2. THE MODELS

Terms and their baseline values are defined in table 1, and the alternative provisioning modes are outlined in figure 1. Behaviour is modelled as a sequence of decisions made at times $t = 1, 2, \dots$. 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. Likewise, the state variables cannot exceed X_{max} or Y_{max} , which represent the maximum levels of 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, following previous formulations (Dall & Boyd 2002), the terminal fitness function is the sum of pay-offs from the parent’s own state, and that of its offspring:

$$F(x, y, T) = \gamma(x) + \theta(y), \tag{2.1a}$$

where

$$\gamma(x) = \begin{cases} 0, & x \leq X_{\text{crit}} \\ \Phi, & X_{\text{crit}} < x \leq X_{\text{max}} \end{cases} \tag{2.1b}$$

and

$$\theta(y) = \begin{cases} 0, & y \leq Y_{\text{crit}} \\ \Omega \frac{y - Y_{\text{crit}}}{y - Y_{\text{crit}} + y_0}, & Y_{\text{crit}} < y \leq Y_{\text{max}} \end{cases} \tag{2.1c}$$

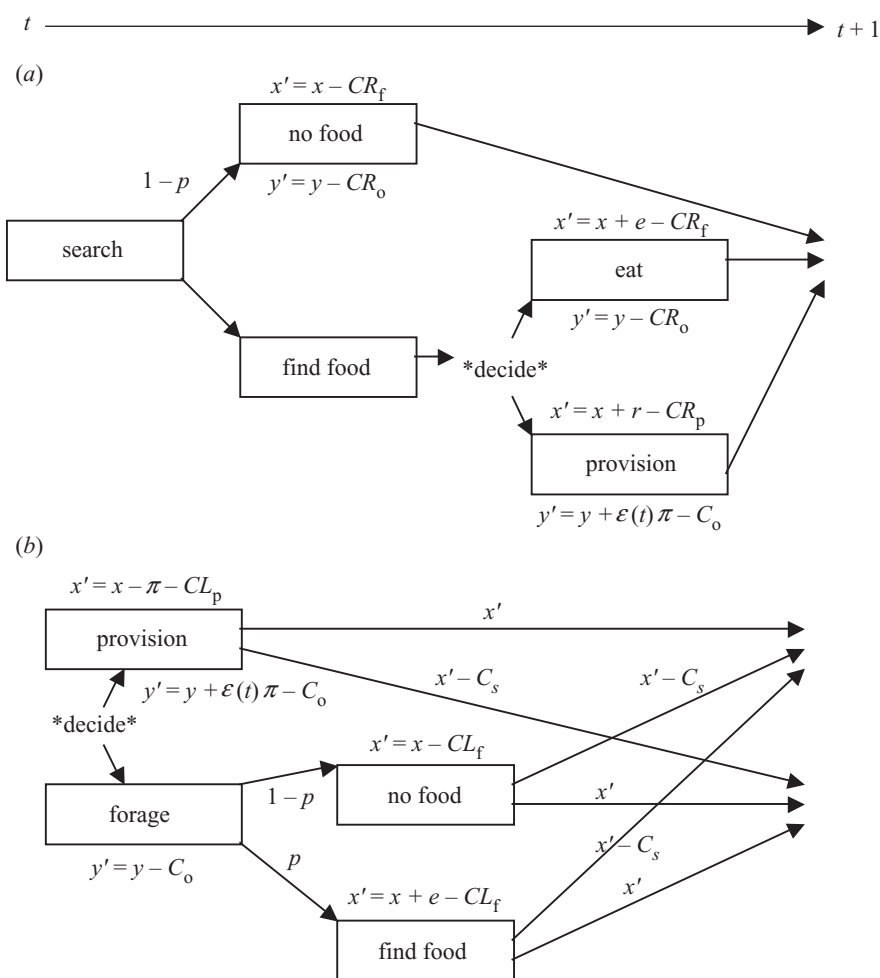


Figure 1. Schematic outlines of the two methods of provisioning for altricial young under energetic risk considered here: (a) regurgitation and (b) lactation. See table 1 for definitions of variables and the text for details. Detailed specification of the models is given in Appendix A.

Φ is the pay-off to the parent for being alive at T , and is therefore a measure of expected future reproduction or residual reproductive value. We assume that this will be insensitive to the state of parental energy reserves at the end of the provisioning period because adults should regain condition rapidly once the stress associated with provisioning is alleviated. However, as is evident from equation (2.1c), we assume that the pay-off from a successful breeding attempt is an increasing, if decelerating, function of offspring state at T . Ω is the limit $y \rightarrow \infty$ of this function, $\theta(y)$, thus representing the maximum possible fitness value of producing independent offspring under current conditions, with $\theta(y) = 1/2\Omega$ when $y = Y_{crit} + y_0$ (Clark & Mangel 2000). In this way, we model the general situation in which body condition at independence has significant consequences for lifetime reproductive success (e.g. Hall *et al.* 2001). However, changing the precise form of this fitness pay-off has little impact on the results we report here because the optimal strategy becomes virtually independent of the terminal fitness function at small t (Houston & McNamara 1999), which is when the differences in the performance of the two modes of provisioning emerge.

At each t , a parent that provisions its dependent offspring via ‘regurgitation’ must search for food (figure 1a). While foraging, we assume that the animal will find food of expected

energetic value e , with probability p , in a time-period, and no food otherwise $(1 - p)$. If it finds food, the parent can decide whether to eat or provision. If it decides to eat located food (or if it fails to find food), it will incur an energetic cost CR_f per time-step, as a result of locating and consuming food where it is found (or searching unsuccessfully for the whole time-period). Alternatively, if the parent decides to provision, it will suffer a metabolic cost CR_p , as a result of locating food, travelling to the central place, provisioning and returning to the foraging habitat. This is in addition to setting aside an amount π of the food found to be provided to its offspring (if alive) at t ; any excess food ($r = e - \pi$) is consumed by the parent, which accounts for the relative time efficiency associated with regurgitation (parents deliver food *and* feed themselves in a time-step: the time it takes to digest food and produce nutritious secretions). If, however, a parent provisions its offspring from its energy reserves (‘lactation’), at each t it can decide whether to be out foraging or remain at the central place to provision (figure 1b). If it decides to forage, the animal has the same prospects as above, and suffers similar metabolic costs CL_f . Alternatively, if it decides to provision, the parent will suffer a metabolic cost CL_p as a result of remaining in the central place with the offspring, in addition to providing energy to its offspring from its reserves at a rate of

π per time-step, if the offspring is alive at t . Because we consider provisioning to a central place, there are additional metabolic costs, C_s , associated with switching activities between time-steps (i.e. travelling to or from the foraging habitat) for this provisioning method. Throughout we assume that $CR_p(\text{search for food} + 2 \times \text{travel to or from central place} + \text{deliver food}) > CR_f = CL_f$ (search for food + consume food or continue searching) $> C_s(\text{travel to or from central place}) \geq CL_p(\text{remain at central place suckling})$.

Regardless of how a parent provisions, however, not all of π will be converted into offspring reserves; some will also be allocated to growth. Therefore, we assume that, if the parent provisions, 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 & Adler 1996), and hence an increasingly smaller proportion of π is converted into offspring reserves over time. Specifically,

$$\varepsilon(t) = \varepsilon_i - \frac{\varepsilon_i t^2}{(kT)^2}, \quad (2.2)$$

where ε_i (regurgitation: $i = R$; lactation: $i = L$) is the proportion of π that is converted to offspring reserves at the start of provisioning (i.e. the baseline efficiency of conversion of available energy into offspring reserves), and k is a constant that specifies the magnitude of ε at T : i.e. $\varepsilon(T) = \varepsilon_i - \varepsilon_i/k^2$. Because energy is lost each time it is converted (e.g. from food to reserves, or reserves to milk), we assume that $\varepsilon_R > \varepsilon_L$ since there are fewer conversions if parents regurgitate the energy they provision. 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.

We find the strategies that maximize the parent's expected fitness at T , specified by equations (2.1), for each mode of provisioning. 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. Because 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 & Clark 1988). We express all results as the proportion of time spent in a given state (for mortality rates and mean state values) or performing a particular action, as determined by direct computation. This was achieved by determining the likelihood that a parent behaving optimally would be in a particular state, or subset of states, at each point in the provisioning period after specifying initial states, X_{init} and Y_{init} (Houston & McNamara 1999). Detailed specification of the models can be found in Appendix A.

3. RESULTS

Provisioning dependent young by regurgitating a portion of located food performs well when the probability of not finding food is relatively low. However, lactation offers a dramatic advantage in terms of the success of a reproductive attempt, as this risk of an energetic shortfall while foraging increases. This is illustrated in figure 2, for which

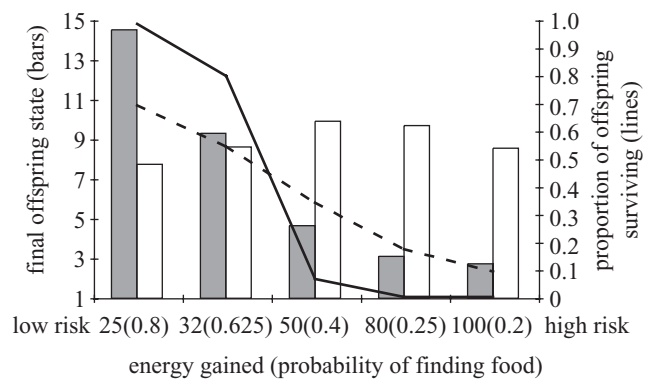


Figure 2. Results from the dynamic optimization models of regurgitation provisioning and lactation outlined in figure 1 showing the effects of varying p , the probability of finding food of expected value e , keeping $\mu = pe = 20$, on the state (bars) and proportion of offspring surviving (lines) at T , the end of the provisioning period. Grey bars and solid line represent outcomes for mothers that regurgitate; open bars and dashed line represent outcomes for lactating mothers; solid line, regurgitation surviving; dashed line, lactation surviving. The values of the other parameters are given in table 1. The pattern shown here is general to our formulation providing certain basic conditions hold. On the one hand, there must be a non-zero probability of raising offspring to independence successfully under both provisioning modes. In addition, the energetic trade-offs must be severe enough that parental and/or offspring survival are not trivial concerns. Finally, the relative metabolic inefficiency of lactating cannot be too extreme (e.g. $\varepsilon_R - \varepsilon_L < 0.29$ for the parameter values outlined in table 1). Note that maternal condition at the start of the provisioning period (X_{init}) has no effect on the qualitative findings we report here.

all fitness accrues from the current breeding attempt; at low levels of risk, offspring show better condition at independence and have a higher chance of surviving if mothers provision by regurgitating food than if they provision their own reserves by lactating. The reverse becomes true as the probability of finding food while foraging declines (all else being equal, including holding the mean amount of food found, μ , constant). This is driven by two factors. When the chance of finding food while foraging is high, regurgitators are free to provision often, while at the same time they can top up their own reserves with any excess food. Mothers that rely on lactation, however, must *either* remain at the central place to provision refuge-bound offspring *or* emerge to forage to top up their energy reserves. This trade-off reduces their efficiency compared with mothers that provision food found directly, in addition to the relative energetic inefficiency of provisioning via lactation (i.e. $\varepsilon_R > \varepsilon_L$). Alternatively, when the probability of finding food while foraging is low (under high risk of an energetic shortfall), mothers that provision directly the food they find are only offered the chance rarely because they must locate food to do so; provisioning by regurgitation is limited by food-finding events. However, mothers that lactate have no such limitation because they provision from their energy reserves; lactation allows prior foraging success to fuel current provisioning, and so provisioning is only limited by maternal reserve levels. This more than compensates for the inefficiency of lactating, and allows mothers to wean

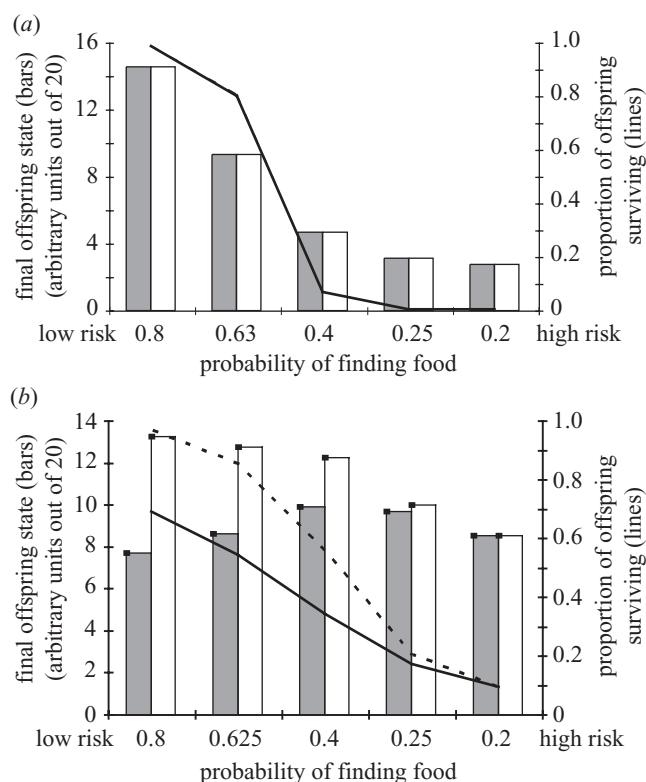


Figure 3. Results from the dynamic optimization models of: (a) regurgitation provisioning and (b) lactation, outlined in figure 1, showing the effects of varying p , the probability of finding food, and e , its expected value ($\mu = ep$), on the state (bars) and proportion (lines) of offspring surviving at the end of the provisioning period, T . (a) For filled bars and solid line, $\mu = 20$; for open bars and dashed line, $\mu = 40$; (b) For filled bars and solid line, $\mu = 20$; for open bars and dashed line, $\mu = 25$. The values of the other parameters are given in table 1.

more young showing better condition than if they provision by regurgitating when food supplies are risky (e.g. $p \leq 0.5$: figure 2). Indeed, the buffering of the ability to provision from actual food-finding events that lactation enables results in subtle strategic responses to the risk of an energetic shortfall. For instance, to survive until offspring can fend for themselves (and gain any fitness pay-off), mothers forage more during the early stages of provisioning to defend higher levels of their own reserves as this energetic risk increases. This puts offspring at risk of starving to death but results in more resources to provision just before independence, and can result in fewer offspring that show better condition under increasing levels of risk (figure 2: open bars and dashed line for $p \geq 0.4$ (Dall & Boyd 2002)).

Because lactation allows mothers to provision even if they fail to find food when foraging, it also allows them to adjust more efficiently their provisioning effort to changes in environmental productivity. This is illustrated in figure 3. The efficiency of provisioning by regurgitating food does not change much if the probability of finding food remains constant but the mean amount of food found changes (even if μ doubles: figure 3a). This is because provisioning is limited by food-finding events, and not the amount of food found, so long as the amount mothers are able to transport back to their offspring is limited, which is

likely in most cases. Indeed, the only component of fitness that regurgitators can adjust to changes in environmental richness *per se* is maternal state at the end of the provisioning period, if it has value.¹ Alternatively, mothers that lactate can improve their provisioning efficiency dramatically as μ increases (even if only by 25%: figure 3b). This is because they can spend more time provisioning as the amount of food found increases; each food-finding event can fuel more provisioning *and* fewer reserves are needed as a buffer against starvation as environmental richness increases (Houston *et al.* 1993).

The main effect of increasing the value of future reproduction relative to the current effort (residual reproductive value) is that it decreases the difference in fitness pay-offs resulting from the two modes of provisioning under energetic risk. This is illustrated in figure 4. Maternal survival is relatively high even when there is no fitness value to adult survival for mothers that regurgitate food to their offspring; even if regurgitators decide to provision the food they find rather than eat it, they will still be able to top up their own reserves with the excess, buffering themselves from starvation and thereby increasing their chance of surviving. When mothers have little or no residual reproductive value this has little impact on the fitness consequences of the fact that being limited by food-finding events results in dramatic declines in the ability to provision young effectively as the risk of not finding food when foraging increases (figures 2 and 4a,b). However, with relatively high residual reproductive value, the high intrinsic adult survivorship associated with regurgitation will temper the fitness consequences of the decreased success of the current brood as energetic risk increases; indeed, the levels of adult survivorship of mothers that lactate become comparable with those associated with regurgitation at high residual reproductive values (figure 4c). However, provisioning from maternal energy reserves allows mothers to adjust adaptively their risk of starving to death to the cost of doing so, mitigating somewhat their relative provisioning inefficiency at low levels of risk (figure 4). Nevertheless, our results suggest that, although the performance of each mode of provisioning improves relative to each other as the future becomes more valuable, the relative fitness pay-off to regurgitating improves more than that to lactating because the relative inefficiency of this provisioning mode will limit the impact of maternal strategic compensation. This suggests that lactation may be most strongly selected for, by allowing mothers to provision offspring independently of variability in their food supplies, in species with few opportunities for reproduction, or in older individuals.

4. DISCUSSION

Our formulation reveals that provisioning to offspring from maternal reserves can offer substantial advantages over provisioning food found directly, despite its relative inefficiency for delivering nutrients to young, when food supplies are risky under a wide range of circumstances (even when more than 25% of the energy is wasted in the process: figure 2). This suggests that the demands of parental feeding by insectivores may have prompted the evolution of true mammals. Parents feeding insects to young face highly patchy and ephemeral food supplies, which, although they can be abundant, are only available relatively

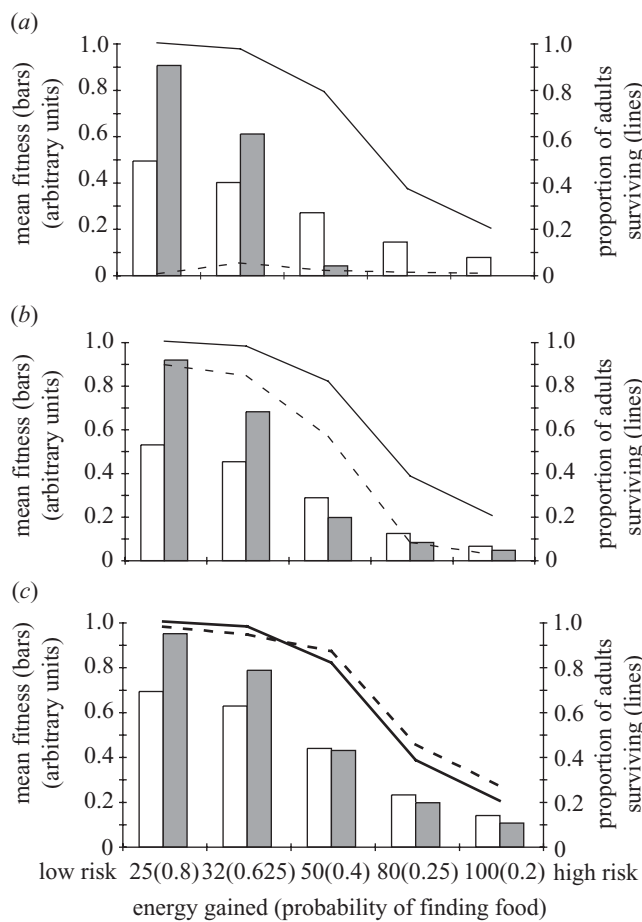


Figure 4. Effects of varying the risk of an energetic shortfall (p and e holding $\mu = 20$; as in figure 2) on the mean fitness pay-off (bars) (scaled to $1 \equiv \Phi + \theta(Y_{\max})$) to, and the proportion of surviving, provisioning adults (lines) when the relative value of the future is varied. Filled bars and solid lines are outcomes for mothers that regurgitate; open bars and dashed lines are outcomes for lactating mothers. Throughout: $\Omega = 50$; (a) all fitness accrues from the current breeding attempt ($\Phi = 0$); (b) the future is worth a quarter of the best current breeding attempt ($\Phi/\theta(Y_{\max}) = 0.25$); and (c) the future is of equal value as the best current attempt ($\Phi/\theta(Y_{\max}) = 1$). The values of the other parameters are given in table 1.

unreliably from one foraging trip to the next (Lack 1968). Therefore, it is likely that there was strong selection for the transition from minimally nutritious proto-lacteal secretions, perhaps produced originally for their anti-microbial properties (Blackburn *et al.* 1989), to fully-fledged milk production and consumption in the insectivorous mammal-like reptiles with extended maternal care (egg incubation and altricial young). Moreover, the metabolic demands of endothermy, once it evolved in the mammalian lineage, will have exacerbated the risk of running a negative energy budget, and hence the unreliability of food resources. The selective advantage associated with being able to provision independently of actually finding food is likely to have been particularly influential for the evolution of lactation if mammalian ancestors were relatively short-lived with few opportunities for reproduction (figure 4). Indeed, recent evidence suggests that at least some mammaliaform reptiles had small body sizes (Luo *et al.* 2002), and many

small extant insectivores have relatively high rates of metabolic turnover (Schmidt-Nielson 1997), which are both associated with short lifespans. In addition, yearly reproductive output and longevity allometries in mammals imply that (all else being equal) the relative reproductive value of each breeding event is likely to be greater for smaller females (Charnov 2001).

Of course the trade-off we explore here is unlikely to be solely responsible for the evident variation in the form and function of lactation across mammalian taxa. Once parental feeding from maternal reserves evolved in the mammalian lineage it is likely that other functional opportunities were created leading to the evolution of a wide range of mammalian traits and strategies (Pond 1977, 1998; Hayssen *et al.* 1985; Blackburn *et al.* 1989; Hayssen 1993). For example, the nutritional quality of milk encourages very rapid postnatal growth, allowing the production of relatively small neonates and early maturation. In addition, providing young with pre-processed food allows jaws to develop fully before teeth are needed, facilitating the evolution of exactly opposable teeth and diets that depend on chewing or grinding food. Indeed, in many herbivorous mammals, because progeny can feed themselves directly from more predictable but low quality resources at a relatively early stage, such functions of milk production may have become primarily important. Moreover, the risk that young are outcompeted or cannibalized by adults is minimized if parents feed young until they reach a significant proportion of adult size, which has been suggested to facilitate the evolution of sociality by encouraging sustained interactions between adults and sub-adults (Pond 1977). Furthermore, the adoption of parental feeding from nutrient reserves also facilitates the exploitation of niches in which resources are both patchy and predictable; when or where conditions are super-productive mothers can maximize the rate at which food is obtained, which allows them to breed under unproductive conditions with minimal impact on their overall nutrient assimilation efficiency. Such task specialization will create opportunities to exploit seasonal environments, and those that are locally very productive but also very dangerous (or very thermally stressful)—like pelagic marine environments—by facilitating breeding migrations to safe (or warm) but unproductive locations.

Nevertheless, our work also has importance beyond the evolution of lactation. In a wide range of carnivorous mammals, including canids, mustelids and pinnipeds, individuals both provision food directly and lactate to young; our models predict that the former should predominate (and/or periods of lactation should be short) when food supplies are reliable because it is more effective than lactation under such conditions, as long as food-patches are rich enough that parents can top-up their reserves *and* set aside food to carry back to their young (which is likely to be true for many predators). In addition, our work suggests an interesting possibility for future study: perhaps there is an optimal switch from regurgitation to lactation with age in such species (particularly the longer-lived ones), as each brood comes to represent a larger and larger proportion of a mother's reproductive value. Moreover, many non-mammals, including insects, fish and birds, feed their young with parental secretions (Clutton-Brock 1991),

and our formulation suggests that such provisioning strategies are more likely to be observed when food supplies are, or become, unreliable. From another perspective, our formulation also suggests that provisioning food directly is likely to be common where resources and suitable breeding sites covary positively in time and space. It is therefore possible to make comparative predictions based on this work. For instance, species that can provision offspring reliably from parental reserves may predominate as a result of anthropogenic activity, with its rapid imposition of conditions that are likely to be suboptimal for many higher vertebrates. Indeed, Columbiform bird species, which can feed their young with 'crop milk' formed from deciduous tissues in the parents' throat, have come to flourish in urban environments where other bird species have failed to persist (Pond 1977).

Furthermore, the importance of risky food access highlighted here may underlie key differences between bird and mammalian life-history strategies. On the one hand, both taxonomic groups are dominated by high levels of offspring altriciality and extended periods of parental care, along with repeated radiations into niches associated with risky access to food. On the other hand, only mammals have opted for provisioning from maternal nutrient reserves as the norm. However, flight imposes severe costs to carrying extra mass (Pennycuik 1996), which may have constrained the widespread adoption of parental feeding from nutrient reserves, particularly if flight preceded compulsory parental feeding in the avian lineage (Burley & Johnson 2002). Yet biparental care is the norm in avian systems; by increasing the number of individuals foraging, this strategy may have offered an alternative means of reducing riskiness in the supply of food to the brood without any concomitant increase in the nutrient reserves required (Giraldeau & Caraco 2000). However, further work is required to ascertain how important this risk-reducing advantage is for the evolution and maintenance of biparental provisioning in birds. Indeed, the relevance of our analysis to this issue is limited because we do not consider reserve-size dependent costs (Witter & Cuthill 1993), nor do we allow pay-offs to provisioning decisions to be dependent on the behaviour of others, which will be the case when there are genetic conflicts of interest between care-givers (Parker *et al.* 2002). Nevertheless, we are confident that appropriate extensions to our analysis, which should involve the application of evolutionary game theory (Maynard Smith 1982), will prove insightful because those bird species showing uniparental female care are associated with food supplies that are relatively reliable (Clutton-Brock 1991) and insectivorous bird species are typically socially monogamous with biparental care (Lack 1968). In addition, the evolutionary success of bat lineages (many of which are insectivorous) suggests that the constraints on provisioning from maternal reserves imposed by flight *per se* are not insurmountable and so detailed analyses of bat provisioning strategies in the light of this work should also provide insights.

In conclusion, we provide, to our knowledge, a first formal demonstration that lactation, by allowing mothers to feed dependent young when food is unavailable, offers substantial selective advantages over provisioning food found directly when food supplies are risky, despite the inefficiencies associated with converting nutrients from

food to reserves and milk. This suggests that the evolution of lactation, a definitive mammalian feature, may have been selected for by the insectivorous lifestyle of oviparous mammal-like reptiles that evolved extensive maternal care.

We thank Joel Brown, Anne Carlson, Tim Clutton-Brock, Tim Coulson, Nick Davies, Sarah Hodge, Rufus Johnstone, Becky Kilner, Andrea Manica, Geoff Parker, Caroline Pond, Colette Wabnitz, Andy Young and two anonymous referees for helpful comments on the manuscript. Thanks also to John McNamara for helpful discussions on how to model 'regurgitation'. S.R.X.D. was supported by a grant (Antarctic Funding Initiative 0003) to I.L.B. and T. H. Clutton-Brock from the Natural Environment Research Council (UK).

ENDNOTE

¹By choosing to 'eat' more often than 'provision' (figure 1), mothers can minimize their metabolic costs without compromising their offspring much more than they already are if food is only rarely found. This only affects fitness when mothers have residual reproductive value (figure 4).

APPENDIX A. DETAILED SPECIFICATION OF THE MODELS

'Regurgitation'

At each t , suppose a parent can choose between two actions: u_1 (eat) or u_2 (provision). If it finds food of amount e , with probability p , and it chooses u_1 (to eat), its state transition is

$$x_{1'} = x + e - CR_f. \quad (\text{A } 1)$$

However, if it chooses u_2 (to provision) and $y > Y_{\text{crit}}$, it provisions an amount, π , of the food and eats the remainder, $r = e - \pi$ if $e > \pi$, or $r = 0$, otherwise. Therefore, its state transition is

$$x_{2'} = x + r - CR_p, \quad (\text{A } 2a)$$

or, if $y \leq Y_{\text{crit}}$,

$$x_{2'} = x + e - CR_p. \quad (\text{A } 2b)$$

However, if it finds no food, with probability $1 - p$, its state transition is always

$$x_{1''} = x_{2''} = x - CR_f. \quad (\text{A } 3)$$

Throughout, $CR_f < CR_p$ are the metabolic costs of foraging and provisioning respectively (see table 1 for details). Meanwhile, if the parent chooses u_1 or if it finds no food, its offspring's state transition would be

$$y_{1'} = y - C_o, \quad (\text{A } 4)$$

whereas, if the parent chooses u_2 and $y > Y_{\text{crit}}$,

$$y_{2'} = y + \varepsilon(t)\pi - C_o \quad (\text{A } 5a)$$

or

$$y_{2''} = Y_{\text{crit}}. \quad (\text{A } 5b)$$

$\varepsilon(t)$ is the proportion of π that is transformed into offspring reserves defined in equation (2.2) and C_o is the metabolic cost to the offspring per time-period.

Let $F(x, y, T)$, defined in equation (2.1), be the fitness of the parent at T . Similarly, $F(x, y, t)$ is its fitness at

$t = 1, \dots, T - 1$. Following equations (A 1) to (A 5), set

$$V_1(x, y, t) = pF(x_{1'}, y_{1'}, t + 1) + (1 - p)F(x_{1''}, y_{1''}, t + 1), \quad (\text{A } 6)$$

and

$$V_2(x, y, t) = pF(x_{2'}, y_{2'}, t + 1) + (1 - p) \times F(x_{2''}, y_{2''}, t + 1) \quad (\text{A } 7a)$$

if $y > Y_{\text{crit}}$, or

$$V_2(x, y, t) = pF(x_{2'}, y_{2''}, t + 1) + (1 - p) \times F(x_{2''}, y_{2''}, t + 1) \quad (\text{A } 7b)$$

otherwise.

'Lactation'

At each t suppose an animal can choose between two actions: u_1 (forage) or u_2 (provision). If it chooses u_1 (to forage), it consumes food of expected energetic value e , with probability p , and nothing with probability $1 - p$. Therefore, its potential state transitions are

$$x_{1'} = x + e - CL_f \quad (\text{A } 8a)$$

or

$$x_{1''} = x - CL_f, \quad (\text{A } 8b)$$

respectively, if the parent foraged at $t - 1$, where CL_f is the metabolic cost of foraging between t and $t + 1$. Alternatively, if the parent provisioned at $t - 1$, $x_{1'} = x_{1'} - C_s$ and $x_{1''} = x_{1''} - C_s$. In addition, its offspring's state transition is always

$$y_{1'} = y - C_o, \quad (\text{A } 9)$$

with C_o being the metabolic cost to the offspring over the time-period. Alternatively, if the parent chooses u_2 (to provision), it suffers a metabolic cost $CL_p < CL_f$ and can provide π units of energy to the offspring from t to $t + 1$. Therefore, if the parent provisioned at $t - 1$, as long as $y > Y_{\text{crit}}$

$$x_{2'} = x - \pi - CL_p. \quad (\text{A } 10a)$$

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

$$x_{2''} = x - CL_p. \quad (\text{A } 10b)$$

Alternatively, if the parent foraged at $t - 1$, $x_{2'} = x_{2'} - C_s$ and $x_{2''} = x_{2''} - C_s$. Equivalently, its offspring's state transitions are

$$y_{2'} = y + \varepsilon(t)\pi - C_o, \quad (\text{A } 11a)$$

or

$$y_{2''} = Y_{\text{crit}}, \quad (\text{A } 11b)$$

respectively, where $\varepsilon(t)$ is the proportion of π that is transformed into offspring reserves defined in equation (2.2).

Let $F(x, y, T)$, defined in equation (2.1) be the fitness of the parent at T . Similarly, $F(x, y, t)$ is its fitness at $t = 1, \dots, T - 1$. Following equations (A 8) to (A 11), set

$$V_1(x, y, t) = pF(x_{1'}, y_{1'}, t + 1) + (1 - p) \times F(x_{1''}, y_{1''}, t + 1), \quad (\text{A } 12)$$

and

$$V_2(x, y, t) = F(x_{2'}, y_{2'}, t + 1), \quad (\text{A } 13a)$$

if $y > Y_{\text{crit}}$, or

$$V_2(x, y, t) = F(x_{2''}, y_{2''}, t + 1), \quad (\text{A } 13b)$$

otherwise.

Dynamic programming equations

In both cases, given equations (A 6) and (A 7), or (A 12) and (A 13), the optimal action $u^*(x, y, t)$ for the parent is then the value of i that maximizes $F(x, y, t; i)$, i.e.

$$F(x, y, t; u^*(x, y, t)) = \max_{i=1,2} V_i(x, y, t; i), \quad (\text{A } 14)$$

and

$$F(x, y, t) = \max_{i=1,2} V_i(x, y, t). \quad (\text{A } 15)$$

REFERENCES

- Blackburn, D. G., Hayssen, V. & Murphy, C. J. 1989 The origins of lactation and the evolution of milk: a review with hypotheses. *Mamm. Rev.* **19**, 1–26.
- Burley, N. T. & Johnson, K. 2002 The evolution of avian parental care. *Phil. Trans. R. Soc. Lond. B* **357**, 241–250. (doi:10.1098/rstb.2001.0923)
- Charnov, E. L. 2001 Evolution of mammal life histories. *Evol. Ecol. Res.* **3**, 521–535.
- Clark, C. W. & Mangel, M. 2000 *Dynamic state variable models in ecology: methods and applications*. New York: Oxford University Press.
- Clutton-Brock, T. H. 1991 *The evolution of parental care*. Princeton University Press.
- Dall, S. R. X. & Boyd, I. L. 2002 Provisioning under the risk of starvation. *Evol. Ecol. Res.* **4**, 883–896.
- Giraldeau, L. A. & Caraco, T. 2000 *Social foraging theory*. Princeton University Press.
- Groenewald, G. H., Welman, J. & MacEachern, J. A. 2001 Vertebrate burrow complexes from the early Triassic Cynognathus Zone (Driekoppen Formation, Beaufort Group) of the Karoo Basin, South Africa. *Palaio* **16**, 148–160.
- Hall, A. J., McConnell, B. J. & Barker, R. J. 2001 Factors affecting first-year survival in grey seals and their implications for life-history strategy. *J. Anim. Ecol.* **70**, 138–149.
- Hayssen, V. D. 1993 Empirical and theoretical constraints on the evolution of lactation. *J. Dairy Sci.* **76**, 3213–3233.
- Hayssen, V. D., Lacy, R. C. & Parker, P. J. 1985 Metatherian reproduction: transitional or transcending? *Am. Nat.* **126**, 617–632.
- Houston, A. I. & McNamara, J. M. 1999 *Models of adaptive behaviour: an approach based on state*. Cambridge University Press.
- Houston, A. I., Clark, C. W., McNamara, J. M. & Mangel, M. 1988 Dynamic models in behavioural ecology. *Nature* **332**, 29–34.
- Houston, A. I., McNamara, J. M. & Hutchinson, J. M. C. 1993 General results concerning the trade-off between gaining energy and avoiding predation. *Phil. Trans. R. Soc. Lond. B* **341**, 375–397.
- Lack, D. 1968 *Ecological adaptations for breeding birds*. London: Methuen.
- Luo, Z. X., Crompton, A. W. & Sun, A. L. 2002 A new mammaliaform from the early Jurassic and evolution of mammalian characteristics. *Science* **292**, 1535–1540.
- Mangel, M. & Clark, C. W. 1988 *Dynamic modeling in behavioral ecology*. Princeton University Press.
- Maynard Smith, J. 1982 *Evolution and the theory of games*. Cambridge University Press.
- Mivart, G. 1871 *On the genesis of species*. New York: D. Appleton.
- Parker, G. A., Royle, N. J. & Hartley, I. R. 2002 Intrafamilial conflict and parental investment: a synthesis. *Phil. Trans. R. Soc. Lond. B* **357**, 295–307. (doi:10.1098/rstb.2001.0950)

- Pennycuik, C. J. 1996 Stress and strain in the flight muscles as constraints on the evolution of flying animals. *J. Biomech.* **29**, 577–581.
- Pond, C. M. 1977 The significance of lactation in the evolution of mammals. *Evolution* **31**, 177–199.
- Pond, C. M. 1984 Physiological and ecological importance of energy storage in the evolution of lactation: evidence for a common pattern of anatomical organization of adipose tissue in mammals. *Symp. Zool. Soc. Lond.* **51**, 1–32.
- Pond, C. M. 1998 *The fats of life*. Cambridge University Press.
- Schmidt-Nielson, K. 1997 *Animal physiology*, 5th edn. Cambridge University Press.
- Stearns, S. C. 1992 *The evolution of life histories*. Oxford University Press.
- Stephens, D. W. & Krebs, J. R. 1986 *Foraging theory*. Princeton University Press.
- Winkler, D. W. & Adler, F. R. 1996 Dynamic state variable models for parental care. 1. A submodel for the growth of the chicks of passerine birds. *J. Avian Biol.* **27**, 343–353.
- Witter, M. S. & Cuthill, I. C. 1993 The ecological costs of avian fat storage. *Phil. Trans. R. Soc. Lond. B* **340**, 73–90.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.