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The evolution of developmental dependence, or 'Why do my kids need me so much?'

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ABSTRACT

Question: The young of some species depend utterly on care by their parents. How does such extreme dependence evolve?

Methods: Dependence is defined as the minimum effort offspring need for survival; thus, greater minimum effort is equivalent to greater dependence. We study a state-dependent life-history model with forward-iterating simulations of a brooding individual. We identify the optimal parental effort given the fitness consequences of that effort for offspring and the offspring's level of dependence. We manipulate the level of dependence and evaluate its effect on parental effort, mean offspring fitness, and mean parental fitness.

Key assumptions: Individual parents must decide daily how many offspring to birth and, consequently, how many remaining offspring will share the parent's acquired resources. A female's offspring all have the same level of dependence. Daily resource availability varies and parents can rear multiple broods in sequence.

Results: Greater altriciality results in smaller broods, larger birth sizes, and prolonged care. The selection gradient on offspring altriciality suggests altriciality can evolve despite negative consequences for parental fitness.

Keywords: altricial, birth asynchrony, brood reduction, developmental dependence, parental care, parental effort.

INTRODUCTION

Altriciality is common in mammals, birds, fish, and insects, but it is a derived condition that is difficult to explain. For example, when altricial birds hatch, they are unable to walk or fly, making them incapable of defending themselves or finding their own food (Nice, 1962). Similarly, marsupial young are born only partially developed and must nurse continuously inside the mother's pouch to complete development (Austin and Short, 1972). Altriciality extends to basic physiological functioning: altricial birds cannot thermoregulate upon hatching (Ricklefs, 1979), embryos of giant water bugs desiccate without paternal attendance (Ichikawa, 1988), and embryos of viviparous elasmobranchs depend upon their

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mothers for osmoregulation (Kormanik, 1992). These altricial young depend on parents for proper development and such dependence can be costly to both parent and offspring. Parental mortality during this period of developmental dependence usually leads to offspring mortality and complete loss of parental fitness. Similarly, parental desertion or abortion of dependent young when conditions are bad also produces complete offspring mortality (reviewed in Clutton-Brock, 1991), which is not conducive for offspring fitness. In this light, it is unclear whose interests are served by altriciality and, therefore, how it evolves.

Altriciality and developmental dependence only occur in species with parental care; therefore, parental care appears to facilitate their evolution. Here, altriciality describes the extent of offspring underdevelopment at, for example, the point when yolk reserves (i.e. pre-fertilization investment) have been consumed, whereas developmental dependence describes the extent to which offspring depend on parental care to make up the difference from that point on. We propose that co-evolution between altriciality, developmental dependence, and parental care has allowed offspring to become more altricial and more dependent as the type, amount, and/or duration of parental care has evolved.

Co-evolution between altriciality, developmental dependence, and parental care is obvious until one considers the challenge in getting the evolutionary process started. We would not expect parents to provide care unless offspring will benefit from it (in other words, unless they are vulnerable), or for altriciality to evolve unless parents are likely to provide care. The critical question is not whether these features emerge through a co-evolutionary process, but how and in which of the possible sequences. We propose that altriciality arises within the context of parents who provide care facultatively. Facultative care means that offspring do not require care for survival and that parents do not always provide care, but when they do, care increases offspring fitness. Under facultative care, parents may respond to the vulnerabilities of offspring – if the environment renders offspring vulnerable, parents provide care; otherwise, they provide no care. We argue that a strategy of facultative care opens the door to the evolution of altriciality because (a) it allows offspring traits to alter the fitness landscape for parental effort, and (b) it eliminates one cost of altriciality for offspring because, barring parental mortality, they are assured some care.

The hypothesis that facultative care and responsiveness to offspring vulnerability may predate the evolution of altriciality has precedents in older arguments developed for patterns in particular taxa. For example, Baylis (1981) developed a similar idea to explain why parental care in fishes is more common in freshwater fishes than marine fishes. He argued that as ancient fishes colonized freshwater, they encountered habitat structure that favoured benthic over pelagic eggs, which in turn favoured territoriality, nest defence, and care of eggs. Although the offspring were still, presumably, precocial during this early stage in care evolution, the environments in which fish found themselves would have favoured parents responding to offspring vulnerability.

In addition, the assumption that the environment influences offspring vulnerability and, consequently, parental effort is supported by numerous studies demonstrating environmental effects on optimal offspring size. For example, Fox and Mousseau (1996) found egg size to influence survival to emergence in seed beetles (*Stator limbatus*) only when eggs were laid in low-quality hosts. In addition, resource levels influence the benefit of large eggs in brook trout [*Salvelinus fontinalis* (Hutchings, 1991)] and the benefit of hatchling size in fire-bellied toads [*Bombina orientalis* (Parichy and Kaplan, 1992)]. In both cases, the effect of size was greater in low-resource environments. To the extent that parental effort influences offspring size via provisioning (Sanz and Tinbergen, 1999; Paitz *et al.*, 2007), incubation (Hepp *et al.*, 2006),

and egg manipulation (Crespi and Lessig, 2004), environments that favour production of larger offspring also could favour parental care activities that increase offspring size, thus providing the pre-existing, facultative care that we expect to facilitate the evolution of altriciality and dependence.

In this paper, we examine how altriciality and developmental dependence influence optimal parental effort and examine the fitness consequences of developmental dependence for parent and offspring. From this, we infer how the co-evolutionary process that produces altriciality can unfold.

OPTIMALITY MODELS OF PARENTAL EFFORT

We build a model of progressive provisioning to offspring in which the parent determines the number of young to birth each day and can adjust brood size throughout the duration of provisioning via birth/brood reduction. Therefore, the parent simultaneously and continuously optimizes offspring number and effort per offspring. The adaptive landscape for parental effort is defined by the trade-off between brood size and individual offspring fitness, which is a function of parental effort per offspring (Smith and Fretwell, 1974; Winkler and Wallin, 1987). Smith and Fretwell (1974) modelled this trade-off and demonstrated that optimal brood size and effort per offspring depend on the shape of the function relating effort per offspring to offspring fitness. They described a function in which offspring fitness increases monotonically with increasing effort per offspring and asymptotes at some maximum offspring fitness. They assumed a minimum effort necessary for non-zero fitness (Fig. 1). Jørgensen *et al.* (2011) recently described a mechanism behind, and empirical support for, these assumptions.

Smith and Fretwell's model has served as a foundation for examining the evolution of parental effort within the context of parent–offspring conflict (e.g. Macnair and Parker, 1979; Godfray, 1995; Mock and Parker, 1998), brood reduction (Bonabeau *et al.*, 1998; Trexler and DeAngelis, 2003), and brood desertion (Sargent, 1990). Indeed, there is a large literature examining the co-evolution of parent and offspring traits (Mock and Parker, 1997; Wolf and Brodie, 1998; Parker *et al.*, 2002; Kölliker *et al.*, 2005; Smiseth *et al.*, 2008). However, this literature focuses on the co-evolution of provisioning and offspring solicitation for resources and not on how the underlying offspring need initially arises or is maintained.

In contrast to earlier models, we evaluate the evolution of the underlying need (i.e. dependence and altriciality) and define it within the framework of Smith and Fretwell's model. Specifically, we assume altricial young require more effort from the parent to have non-zero fitness than do precocial young. In other words, the x-intercept of the offspring fitness curve increases as dependence increases (Fig. 1). We evaluate how selection acts on dependence by determining how changes in the intercept of this fitness function affect offspring fitness, given that parents provide the optimal level of effort.

Recently, Kindsvater and colleagues (Kindsvater *et al.*, 2010, 2011) used dynamic programming to describe changes in maternal allocation to offspring size versus number as females age, when offspring survival is negatively density-dependent. To incorporate density dependence, they manipulated the shape of the function relating offspring size to offspring fitness and found that as the negative effect of density on survival increases, females produce fewer, but larger, offspring (Kindsvater *et al.*, 2010). We apply a similar method of manipulating the offspring fitness function and using dynamic programming to evaluate the consequences for maternal investment.

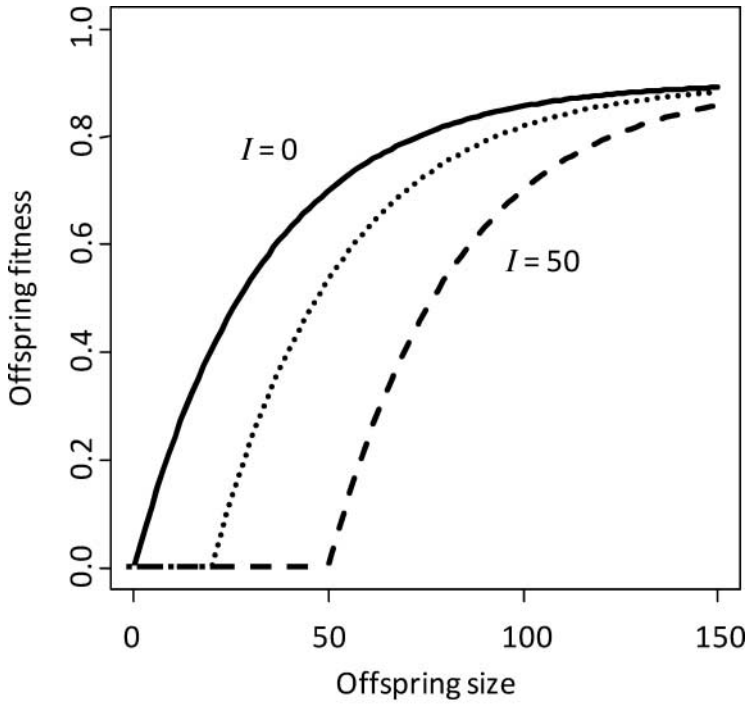

Fig. 1. Offspring fitness is a function of size at birth, which is determined by the cumulative parental effort received before birth. Following Winkler and Wallin (1987), I determines the minimum effort required for survival and k determines the rate of increase (here held constant at 0.03).

Our approach resembles the arguments advanced by Eshel and Feldman (1991) in their exploration of begging handicaps. Eshel and Feldman (1991) showed that offspring could manipulate parents into providing more care at the expense of future offspring. Their model assumes an asymmetry in the marginal benefit of parental provisioning (i.e. different offspring fitness curves) between current and future offspring that favours investing more into current offspring. In contrast, we examine intra-brood conflict over resources and show that the asymmetry assumed by Eshel and Feldman (1991) is not necessary for the evolution of costly parental care. We focus on intra-brood conflict when all offspring offer parents the same marginal benefit and when an increase in the amount of effort per offspring can only occur through the death of some offspring. This approach allows for a conservative study of the circumstances under which dependence and altriciality could evolve; if increased developmental dependence is favoured even when it increases the offspring's own risk of being abandoned, then it is predicted to evolve when the risk is imposed entirely on future siblings, as well.

MODEL OF DEVELOPMENTAL DEPENDENCE

We build a state-dependent life-history model (Mangel and Clark, 1988; Mangel and Ludwig, 1992; Houston and McNamara, 1999; Clark and Mangel, 2000) of progressive provisioning by a parent that can reproduce multiple times within a reproductive period of length T, but at the end of the

period acquires no additional reproductive success. We consider a female that gestates a brood of offspring and can give birth to all or a portion of her brood on each day during gestation. The longer the female gestates young before giving birth, the larger young are at birth and the higher their probability of surviving to maturity. Using the rate-maximizing approach developed by Mangel (1987) to determine the optimal egg-laying behaviour of a parasitoid across a finite time horizon, we evaluate the number of offspring the female must birth each day over a reproductive season, given brood size and current offspring size. We assume the language of a matrotrophic female, although the model applies to any parent that provisions its young after fertilization.

We consider a parent who at time t is carrying $N(t)$ identical offspring of size $S(t) = s$. If she births b of these offspring, then

$$N(t+1) = N(t) - b, \tag{1}$$

and she receives an increment in lifetime fitness that is the product of the number of offspring she births times their expected survival to maturity, $bW_{\mathrm{O}}(s)$. $W_{\mathrm{O}}(s)$ is a saturating function of offspring size described by (Smith and Fretwell, 1974; Winkler and Wallin, 1987) (Fig. 1):

$$W_{\mathrm{O}}(s|k, I) = 1 - e^{-k(s-I)}, \tag{2}$$

where k determines the slope of the function, and I is the minimum size required for offspring survival (i.e. the right-hand side of equation 2 is set equal to 0 for $s < I$). In this framework, I defines the extent of developmental dependence; greater developmental dependence is indicated by larger I. If offspring are born smaller than the minimum for survival (i.e. if $s < I$), they make no contribution to parental fitness and are equivalent to underdeveloped, aborted young.

The remaining offspring continue to grow during period t. If $E(t)$ denotes the energy available for offspring growth during period t, then

$$S(t+1) = S(t) + \frac{E(t)}{N(t) - b}, \tag{3}$$

with the understanding that growth only applies when $b < N(t)$. When $b = N(t)$, the female immediately fertilizes a new clutch of n_0 eggs of initial size s_0 and allocates the energy available during t to this brood.

We assume J discrete energy states for the environment and that

$$\Pr\{E(t) = E_j\} = p_j, \tag{4}$$

where p_j is a discrete normal distribution, i.e. $p_j = c_n e^{-\left(\frac{(E_j-\mu)^2}{2\sigma^2}\right)}$ with c_n chosen so that $\sum_{j=1}^{J} p_j = 1$.

We let $W_{\mathrm{P}}(n, s, t|k, I)$ denote the parent's maximum expected accumulated reproduction from brooding offspring, given that $N(t) = n$ and $S(t) = s$. Then $W_{\mathrm{P}}(n, s, T|k, I) = 0$, since no reproduction can be accumulated after the end of the season. Because $N(t+1)$ and $S(t+1)$ will depend on whether a female has birthed her entire brood, we define an indicator function, D_x such that

$$\begin{aligned} D_x &= 0 \text{ if } (x > 0) \\ D_x &= 1 \text{ if } (x = 0) \end{aligned}.$$

Then, for previous times ($t < T$), we have (Mangel and Clark, 1988; Clark and Mangel, 2000):

$$W_{\mathrm{P}}(n, s, t|k, I) = \sum_{j=1}^{J} p_j \max_b \left\{ b W_{\mathrm{O}}(s) + (1 - D_{n-b}) e^{-m} W_{\mathrm{P}}\left(n - b, s + \frac{E_j}{n-b}, t+1 \right) + D_{n-b} e^{-m} W_{\mathrm{P}}\left(n_0, s_0 + \frac{E_j}{n_0}, t+1 \right) \right\}. \quad (5)$$

The first variable on the right-hand side, p_j, indicates that the sum is taken over all possible energy states encountered by the parent. The first term within the brackets is the immediate increment in reproduction from offspring that were born during t. The second term is the average (over future energy states encountered) future accumulated reproduction, multiplied by the probability of survival during period t if the female births none or only part of her brood, denoted by e^{-m}, where m is the mortality rate. The third term is the future fitness if the entire brood is birthed and she begins with a new clutch of n_0 eggs of size s_0.

We identify the optimal number of offspring to birth, $b^*(n, s, E_j, t|k, I)$, given each possible combination of brood size and offspring size at each step through gestation using equation (5). We start at $T-1$ and solve backwards through time to $t=1$. Once $b^*(n, s, E_j, t|k, I)$ has been calculated across all values of n and s, we iterate the model forward to simulate the resource allocation decisions of a gestating female in an environment in which daily resource availability is stochastic. To incorporate stochasticity in resource availability, we draw a uniformly distributed random variable U and find the j satisfying

$$\sum_{j'=0}^{j-1} p_{j'} < U \leq \sum_{j'=0}^{j} p_{j'}.$$

We then determine E_j (equation 4) and use this value to identify $b^*(n, s, E_j, t|k, I)$ and to calculate $S(t+1)$ using equation (3). During forward iteration, $S(t)$ can assume values for which $b^*(n, s, E_j, t|k, I)$ has not been calculated. This occurs because, during the backward-running optimization, $b^*(n, s, E_j, t|k, I)$ was identified for discrete combinations of $S(t)$, $N(t)$, and t, whereas during forward iteration, $S(t)$ is a continuous variable. Because $b^*(n, s, E_j, t|k, I)$ can only take integer values, linear interpolation (Clark and Mangel, 2000) would not provide a biologically meaningful result. Instead, we find the r' that satisfies

$$s_{r'} \leq S(t) < s_{r'+1}$$

and then identify $b^*(n, s, E_j, t|k, I)$, where

$$s_r = \max\{s_{r'}, s_{r'+1}\}.$$

We assume that the extent of developmental dependence varies across, but not within, broods. We assume that dependence is the same across all individuals within a brood. For each of 5000 forward simulations, we identify the average number of offspring born simultaneously (i.e. cohort size), the average duration of care, average offspring size at birth, parental fitness (W_{P}), and average individual offspring fitness (W_{O}). We evaluate the relative fitness of individuals that exhibit different levels of dependence and assume that selection will favour the level of dependence that confers the highest offspring fitness. A summary of the variables, definitions, and their ranges is provided in Table 1.

Table 1. Definitions of variables, default values, and possible ranges

Variable	Definition	Value or range
T	Time horizon; duration of gestation	31 days
E	Daily energy intake, a stochastic variable	~N(10,5)
n	Brood size at the start of t, state variable	1–10
s	Embryo size at the start of t, state variable	0–200
b	Number of embryos born during t	0–n
b*	Maternal optimum number of embryos to birth	
I	Minimum size at birth necessary for survival	2–50
k	Slope parameter of offspring fitness function	0.01–0.1

RESULTS

Birth cohort size, birth size, and duration of care

Increasing developmental dependence by increasing the minimum size for offspring survival (I) changed the optimal value of several traits. Cohort size, the number of young born simultaneously, decreased to a single individual as the level of dependence increased beyond the bare minimum (Fig. 2). Both the size of offspring at birth (Fig. 2) and the duration of care, or gestational age (Fig. 3), increased steadily with increasing level of dependence. These patterns were qualitatively similar whether energy availability was deterministic or stochastic and were visible across a range of values for k, which is the parameter that describes how rapidly offspring fitness increases with size at birth (results not show).

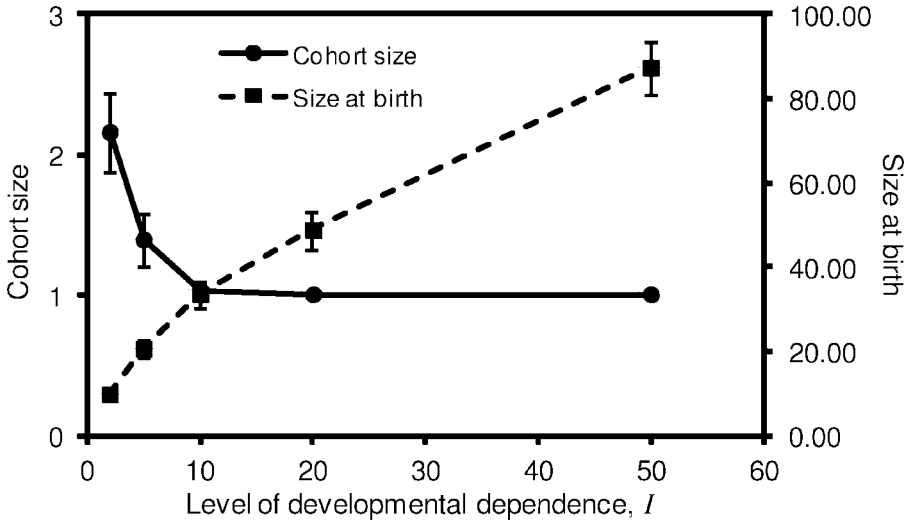

Fig. 2. Mean (±S.D.) offspring size at birth and number of offspring born in a cohort for 5000 forward simulations. The greater the dependence of offspring on parental care, the greater offspring birth size but the fewer offspring born to females over the time horizon. $E_t = 10 \pm 5$ S.D.

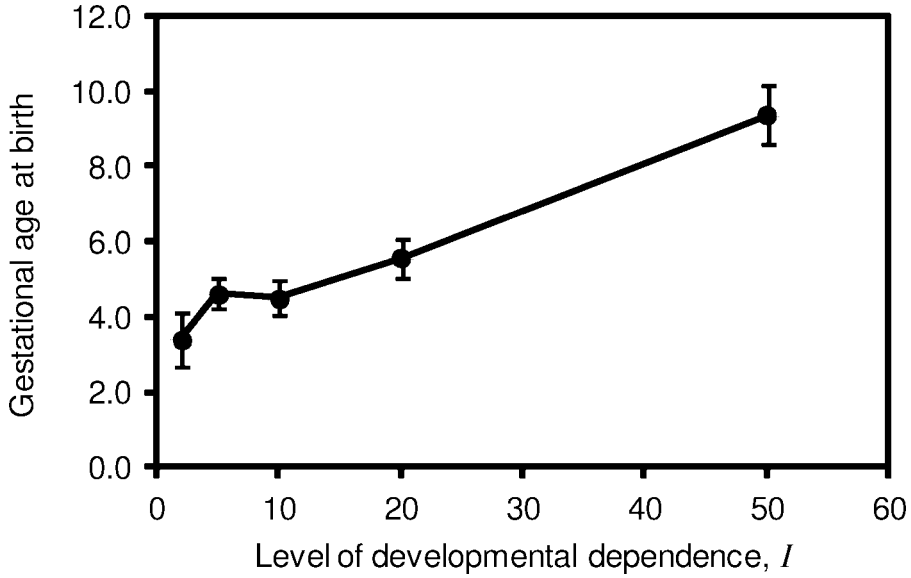

Fig. 3. Mean (±S.D.) gestational age of young at birth. Young with greater developmental dependence have been brooded older when born, indicating that parents provide care longer the greater the dependence of young. $E_t = 10 \pm 5$ S.D.

Birth asynchrony, offspring desertion, and parental survivorship

The number of eggs fertilized ranged from one to ten and was variable among successive broods of the same female. The lower the level of developmental dependence (I), the higher the median number of eggs fertilized. In addition, when more than one egg was fertilized, offspring were born a few at a time (i.e. birth was asynchronous). The results were similar regardless of whether energy availability was constant or stochastic. These results suggest that asynchronous birth was not a response to variable energy availability. Females fertilized more eggs later than they did early in the season, regardless of whether energy was constant or variable.

When birth is asynchronous, offspring are necessarily born at different gestational ages and at different sizes. However, one can predict the size of offspring that return the greatest fitness benefit per unit effort for the mother [e.g. graphically, as in Smith and Fretwell (1974) and Charnov (1976); mathematically, as in Clark and Mangel's (2000) single host maximum]. For each level of developmental dependence, we compared this optimum to the actual size of offspring at birth and found that offspring were always born larger than the minimum size for survival and were, on average, slightly smaller than the size that would return the greatest benefit to the mother's fitness (Table 2).

Resource availability

We evaluated the effect of different levels of daily resource availability E_t when there was no stochastic variation around each level. Increasing the daily energy intake resulted in larger birth cohorts, shorter gestation, and more young born over the time horizon. However, average size at birth was not affected by energy availability. Optimal size at birth is

Table 2. Mean (S.D.) realized dynamic optimal size was always greater than the minimum for survival and slightly smaller than the static optimum predicted by the model of Smith and Fretwell (1974)

Minimum size, I	Static optimal size*	Mean realized dynamic optimal size
2	13	11.09 (1.00)
5	22	21.46 (1.35)
10	33	33.91 (2.36)
20	51	48.54 (3.57)
50	95	86.70 (4.89)

*Optimal birth size corresponds to the offspring size at birth for which the marginal benefit for the mother is greatest, i.e. the value of S for which $dW_O/dS = 0$.

Note: $k = 0.03$, $m = 0.105$, and $E_t = 10 \pm 5$ S.D.

determined by the level of dependence, not resource availability, so parents adjust the duration of care as resource availability changes so as to achieve the optimum birth size.

Selection on developmental dependence

Offspring fitness increased rapidly with the initial increase in developmental dependence but the advantage of further increases in dependence diminished above $I = 10$ (Fig. 4). The effect of dependence on parental fitness was the opposite; parental fitness declined rapidly as dependence increased from 2 to 10, but showed little decline when $I > 10$. These results suggest that selection on relatively independent offspring will favour, at least initially, greater dependence, which will result in smaller birth cohorts, larger birth sizes, and prolonged care. However, this increase in dependence is unlikely to continue indefinitely.

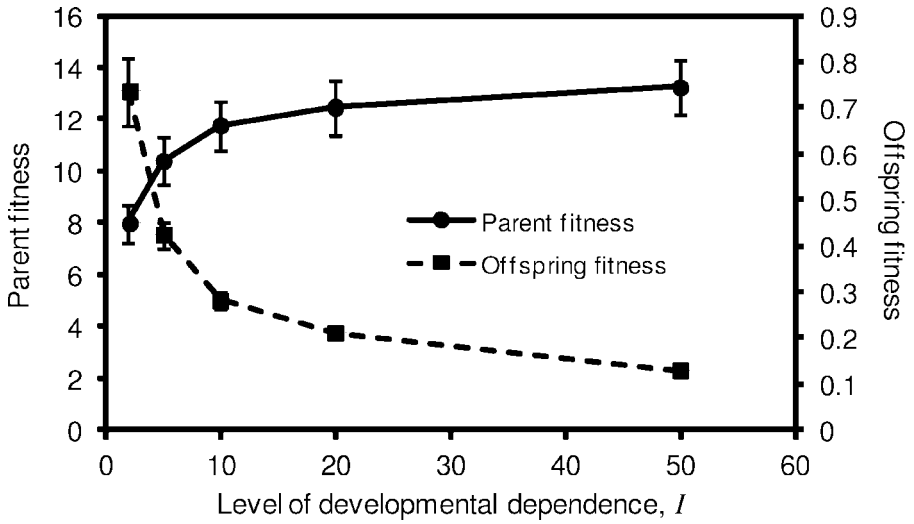

Fig. 4. Mean (±S.D.) fitness for parents and offspring for 5000 forward simulations. Offspring fitness is the probability of survival to maturity. Parental fitness is the sum of the fitnesses of a female's offspring. $E_t = 10 \pm 5$ S.D.

The relatively small effects of dependence on offspring and parental fitness when $I > 10$ suggests that intermediate levels of dependence will evolve readily but that it would be difficult in this model for extreme dependence to emerge.

The selection favouring greater dependence is stronger when fitness increases rapidly with increases in offspring size at birth (high values of k: Fig. 5A). To appreciate this point, recall that when fitness increases more rapidly with offspring size (i.e. when k is larger), offspring born at any particular size have higher fitness than offspring of that size would have when k is smaller. From the female's perspective, higher values of k more strongly discourage an increase in investment per offspring and encourage investment in more offspring (Fig. 5B).

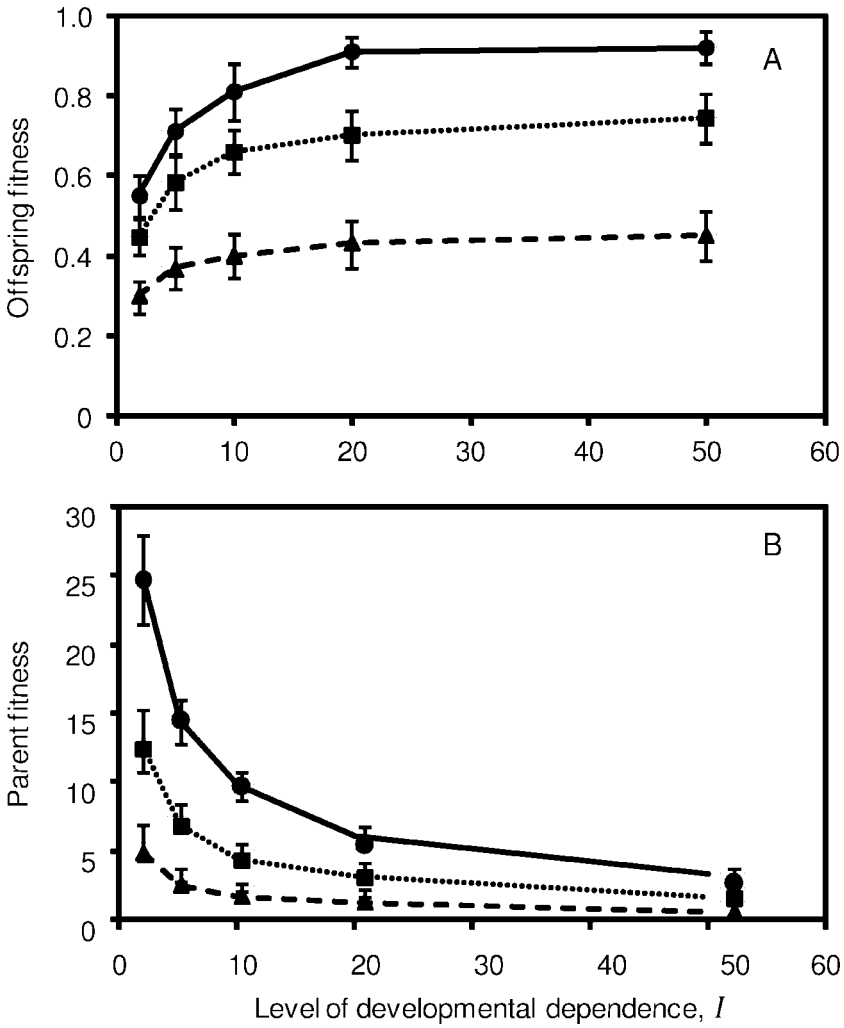

Fig. 5. Mean (±S.D.) fitness of (A) offspring and (B) parents for 5000 forward simulations. The slope of the fitness function, k, had little effect on the qualitative result that selection on offspring and parents favours more and less dependence, respectively. ●, $k = 0.10$; ■, $k = 0.03$; ▲, $k = 0.01$. $E_t = 10 \pm 5$ S.D.

Table 3. Mean (S.D.) effects of the parameter describing the slope of offspring fitness as a function of offspring size at birth on life-history traits for 5000 simulations

	Slope parameter, k		
	0.01	0.03	0.1
Size at birth	33.87 (2.67)	21.46 (1.35)	13.76 (0.73)
Birth cohort size	1.00 (0.006)	1.10 (0.096)	2.19 (0.28)
Total offspring born to parent	7.28 (0.74)	11.82 (0.93)	18.88 (1.60)
Age at birth*	4.84 (0.36)	4.82 (0.42)	5.08 (0.43)
Eggs fertilized	1–3	1–4	1–6

*Age at birth indicates the gestational age of young when born and is a measure of the duration of parental care.

Note: $I = 5$, $m = 0.105$, and $E_t = 10 \pm 5$ S.D.

Indeed, in the classic Smith and Fretwell (1974) model, higher values of k are associated with smaller size at birth and more offspring; we obtained these same patterns when we increased k (Table 3). But it is precisely in this situation, when k is high, that dependence confers its greatest benefit, because it coerces greater investment in a context when there is little reason for the parent to increase that investment. Thus we found that the advantage of greater dependence (indicated by the slopes of the curves in Fig. 5) was small when k was its lowest value but quite high when k was high. However, even at higher values of k, there was little benefit of further increases in dependence beyond $I = 20$, suggesting that under our model we always expect at least intermediate levels of dependence to evolve and to evolve more rapidly when k is high, but we do not expect extreme dependence to evolve.

DISCUSSION

We found that offspring development can influence parental investment. Greater developmental dependence (increasing I) favoured parents investing more resources per offspring and fertilizing fewer eggs. This is particularly so when offspring fitness increases rapidly with size at birth (high values of k). This change in investment pattern occurred because a change in offspring development caused a change in the fitness landscape for parental effort, increasing the optimal effort as developmental dependence increased. In effect, our results suggest that mutations in offspring development that increase dependence will alter the marginal benefit of added care and thereby initiate the co-evolutionary process, which, eventually, produces the association between altriciality and extensive parental care.

In our model, females never aborted non-viable (i.e. smaller than minimum size) embryos and they typically birthed offspring smaller than the size that would maximize the female's fitness return per effort in individual offspring. This result is similar to that found by Clark and Mangel (2000) when they compared predictions of their single host maximum model of parasitoid oviposition with those of a rate-maximizing model. When female fitness is determined by the number or quality of offspring produced cumulatively over some period of time, as opposed to during one reproductive event, the female is predicted to allocate less effort during each individual event in return for greater cumulative fitness gain.

Birth asynchrony, in which some offspring were born earlier and smaller than others in their cohort, occurred when dependence was low and initial brood size was large. Birth asynchrony was an unexpected result of our model; this may be analogous to brood reduction, in which the offspring that are abandoned survive initially, though with reduced likelihood of long-term survival. In this context, the pattern we observe is consistent with existing models linking parental investment, brood size, and brood reduction. For example, O'Connor (1978) predicted brood reduction to be more likely for mothers of large broods than small broods, consistent with our result that birthing asynchrony occurred with larger broods, and consistent with data from birds (O'Connor, 1978) and plants (Uma Shaanker *et al.*, 1988).

We contend that developmental dependence can evolve through its effect on the relationship between parental effort and offspring fitness. Specifically, our model predicts that the evolution of offspring traits towards greater dependence can cause parents to increase per-offspring investment. This is especially the case in contexts when the relationship between offspring size and offspring fitness would otherwise promote lower per capita investment by parents (more rapid increases in offspring fitness with size at birth, or higher values of k in our model). This process is analogous to direct manipulation of parental investment by offspring via siblicide and begging (for reviews, see Mock and Parker, 1997; Hinde and Kilner, 2007). However, the evolution of developmental dependence as a means of manipulating the distribution of resources among brood mates is strikingly different than manipulation via siblicide and begging, mechanisms that have been explored in depth both experimentally and through modelling (e.g. Macnair and Parker, 1979; Godfray, 1995; Bonabeau *et al.*, 1998). For example, in begging and the aggression that results in siblicide, brood mates compete directly with one another. Asymmetries in begging intensity and aggression, such as that created by hatching asynchrony (Mock and Parker, 1997), result in asymmetries in the underlying marginal benefits of parental effort and, therefore, in parental resource allocation. In contrast, our model shows that developmental dependence can evolve without any asymmetries among offspring. Indeed, we assume brood mates have identical underlying fitness functions (Fig. 1), begin development at the same time, and face the same risk of early birth. Even without asymmetry among brood mates, greater developmental dependence is predicted to evolve because it ensures greater parental effort per individual offspring.

The evolution of developmental dependence here is perhaps most similar to the analytical treatment of the evolution of a begging handicap by Eshel and Feldman (1991). We found that developmental dependence can evolve because dependent offspring elicit more resources from the parent, resulting in higher offspring fitness, despite the fact that female fitness declines with greater dependence. This outcome is similar to the conditions for the evolution of a begging handicap. Eshel and Feldman demonstrated that, if a parent's offspring all exhibit the same costly begging, then even though parents with such offspring have lower fitness than parents with 'normal' offspring, costly begging evolves because it increases the fitness of the offspring themselves. In effect, offspring change the fitness landscape for the parents' distribution of resources so that parents are doing the best they can, given the circumstance of costly begging. Although Eshel and Feldman's (1991) model differs from ours in several respects (e.g. their brood size of one and assumption that total investment per brood could vary), the manner in which their begging handicap and our developmental dependence manipulate the landscape of parental fitness is identical.

One line of evidence consistent with our hypothesis that evolving offspring traits can shape the fitness landscape of parental investment comes from a comparative study

indicating that developmental dependence precludes the loss of care in matrotrophic (i.e. viviparous with extensive gestational investment) fishes. In teleosts, parental care has evolved in lineages lacking care numerous times (Gittleman, 1981; Gross and Sargent, 1985). Complete losses have occurred often (Gross and Sargent, 1985), but rarely in those groups in which offspring dependence on care is high, such as in viviparous, and specifically matrotrophic, species. A study of the distribution of viviparity in Atherinomorph fishes concluded that viviparity has not been lost from any of the four families in which it occurs (Mank and Avise, 2006), and the authors suggested that losses may be precluded by the physiological and morphological adaptations associated with internal fertilization and livebearing, imposing a sort of 'evolutionary ratchet'. Comparison with other groups of viviparous species suggests that losses of viviparity in fishes may be precluded by high offspring dependence instead of viviparity itself. Indeed, while viviparity has evolved repeatedly in fishes (Lydeard, 1993; Meyer and Lydeard, 1993; Mank and Avise, 2006) and reptiles (de Fraipont *et al.*, 1996) and there have been losses of viviparity within reptile clades (de Fraipont *et al.*, 1996), there have been no losses of viviparity within clades of fishes that are also matrotrophic (Reznick *et al.*, 2002). These data suggest that embryo dependence on matrotrophy has altered the maternal fitness landscape so much that losses of viviparity are nearly impossible.

The evolution of parental effort and altriciality/developmental dependence formalized by our model complements these earlier studies demonstrating offspring influence over parental allocation of resources, while it describes an evolutionary process that could give rise to the extreme developmental dependence characteristic of many species. In doing so, our model bridges offspring manipulation of parental effort as understood through conflict models and the more pattern-driven examination of parental care and offspring traits across broad groups of taxa. In merging these two approaches, we show how developmental dependence can be an adaptive strategy for offspring. Namely, that despite being inherently more vulnerable if their parents desert them or are killed, developmentally dependent offspring gain considerably because they are assured a high level of care. Therefore, developmental dependence appears to serve the interests of offspring and evolves in conflict with parental interests while guaranteeing high parental effort. To reverse the colloquialism, offspring evolve developmental dependence while dragging parents along kicking and screaming.

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