A theoretical analysis of the energetic costs and consequences of parental care decisions

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Should a parent care for its young or abandon them before they reach independence? We consider parental care behaviour as an adaptive decision, involving trade-offs between current and future reproduction. The condition of the parent is expected to influence these trade-offs. Using a dynamic programming model we explore how changes in the levels of energetic reserves, and time in the season, determine changes in parental care decisions. The novel feature of our model is that we have included the possibility of remating within the current breeding season in a consistent manner by explicitly modelling the behaviour of unmated animals. We show that there may be several fluctuations in the average duration of care during the breeding season. We also show that, because of the dependence of parental care behaviour on both the condition of the parent and time during the breeding season, changing some of the costs of care may increase the duration of care during one part of the season and decrease it at another. The model also shows that the conditions prevailing for animals with dependent offspring can affect the way in which an unmated animal behaves. For example, the behaviour of unmated animals may change to compensate (partly) for increases in the costs of raising offspring, which are produced at a later date (for example, by increasing the duration of foraging between breeding attempts). Overall, the model provides a good framework for understanding how various ecological and life-history variables should influence parental care behaviour during a breeding season.

Keywords: desertion; parental care; dynamic optimization

1. INTRODUCTION

The care of offspring is a behavioural pattern observed in many animals. One or both parents guard and incubate the eggs, or brood and feed the young in several invertebrates, fishes, amphibians, reptiles, birds and mammals (reviewed by Clutton-Brock 1991; Davies 1991; Rosenblatt & Snowdon 1996). When animals terminate parental care before the full independence of the young, they are said to 'desert' their offspring and this term is used without any restriction to a particular mating pattern, such as monogamy or polygyny (Fujioka 1989; Székely *et al.* 1996). Desertion is often viewed as aberrant behaviour; however, many researchers have argued that the desertion of offspring should be understood as an adaptive decision (for a review, see Székely *et al.* 1996). In this framework, parental care decisions are made on the basis of whether or not it is optimal to continue to care for young. Opting for biparental or uniparental care can thus be regarded as limiting the range of desertion decisions. For example,

uniparental care is just the result of one parent making the adaptive decision to desert before providing any care at all.

The basis for modelling parental care and offspring desertion as adaptive decisions lies in the standard life-history trade-off between current and future reproduction (Roff 1992; Stearns 1992). The term 'future reproduction' can mean the broods that may be raised in the next breeding season, the broods which may be obtained through remating in the current breeding season, or both. Remating following desertion within a single breeding season has been observed in many animals (e.g. insects: Olmstead & Wood (1990); fishes: Keenleyside *et al.* (1990), Balshine-Earn (1995); birds: Beissinger & Snyder (1987), Fujioka (1989), Persson & Öhrström (1989), Székely & Cuthill (1999), Pilastro *et al.* (2001); mammals: Hiraiwa-Hasegawa & Hasegawa (1988)). Opportunities for remating are constrained by the time left within a breeding season (Beissinger & Snyder 1987; Reid & Roitberg 1995; Székely & Cuthill 2000), leading to a time-dependence in this trade-off. A reduction in the probability of survival to future breeding seasons necessarily entails a loss of future reproductive success. Providing care for offspring may have a detrimental effect on an adult's survival prospects by reducing fat reserves because of a reduction in the time available for feeding (Clutton-Brock

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1991; Sabat 1994). In birds and mammals it has been observed that parents desert their offspring when food is in short supply (reviewed by Clutton-Brock 1991; Székely *et al.* 1996).

The existence of these two different reasons for desertion means that general models of desertion should be both state- and time-dependent (Sargent 1990; Kelly & Kennedy 1993). We describe a stochastic dynamic optimization model (Houston *et al.* 1988; Mangel & Clark 1988; Houston & McNamara 1999; Clark & Mangel 2000) in which an animal's breeding opportunities are limited to a well-defined breeding season and the value of subsequent breeding seasons is represented by a state-dependent fitness increment at the end of the season. An individual with offspring faces a sequence of decisions about whether to continue with parental care or to desert. Using dynamic programming, we find an optimal strategy, which specifies whether an animal should desert or care depending on its energy reserves, the age of its offspring, and the time left until the end of the breeding season. From this we derive the probability that offspring will be deserted at a given age and time, and the average duration of parental care in the population. Our model allows for the possibility of remating within the current breeding season, and the number of breeding attempts made by an individual within a season is determined by its pattern of care and desertion. Between breeding attempts, animals may spend some time feeding in order to increase their chances of successfully rearing the next brood. We explicitly model the behaviour of unmated animals, and show how the time spent feeding may depend on the costs of care.

We have made two major simplifying assumptions. First, broods or litters have a fixed size, which does not vary, either between matings for a given individual, or between individuals in the population. The consequences of variable brood sizes have been considered elsewhere (Taborsky 1985; Székely *et al.* 1996). The second simplification is that we have looked at the decision of one parent without considering the response of its mate. In cases where the deserters are typically all of one sex this may be a useful approximation. For example, in several species of bird, such as ducks, grouse and hummingbirds, males are not involved in incubation or brood care, whereas desertion by females is common in ratites and shorebirds (Lack 1968; Clutton-Brock 1991; Reynolds & Székely 1997). In a few fish, amphibian and bird species either parent may desert the clutch or brood (Balshine-Earn 1995; Székely *et al.* 1996; Bourne 1998) so, clearly, a game-theoretical treatment is required for an understanding of parental care decisions across all species. However, existing game-theoretical models (Maynard Smith 1977; Grafen & Sibly 1978; Lazarus 1990; Yamamura & Tsuji 1993; Balshine-Earn & Earn 1997; Webb *et al.* 1999; McNamara *et al.* 2000) consider neither the energetic consequences of care nor the effects of the behaviour of animals without young.

In § 2 we describe the state-dependent dynamic optimization model. The results presented fall into two categories. (i) There are some intuitive results. These help to establish confidence in the remainder of the results. (ii) There are also results that are interesting or unexpected. The parameter values used were chosen to provide clear examples of the effects that we discuss. Finally, we

discuss our theoretical results in relation to observed parental care behaviour.

2. THE MODEL

The model is a schematic description of the behaviour of an individual attempting to breed during a time interval $0 \leq t \leq T$, where 0 and T mark the beginning and end of the breeding season. The energy reserves of the adult at time t are described by a random variable, $X(t)$, which can take integer values between zero and some maximum value $X_{\max}$. If these reserves fall to zero at any time then the adult is assumed to have died of starvation. In addition to energy reserves, the state of an adult is described by a deterministic variable $a(t)$, which is related to the age of any young. The state variable $a(t)$ can take integer values between zero and a maximum A , which is the age at which the young become independent. An adult without any dependent offspring at time t has $a(t) = 0$.

The time-period $[0, T]$ is divided into unit intervals, which we will call 'days', and we consider how a sequence of actions at times 0, 1, 2, ..., $T - 1$ affects the animal's state. We distinguish between adults without dependent offspring ($a = 0$) and parents ($a > 0$). If the animal has no offspring at the beginning of day t , then $a(t) = 0$. If the animal does not find a mate, then $a(t + 1) = 0$. However, if it does find a mate during that day, we assume that offspring are produced on the day of mating and that $a(t + 1) = 1$. Thereafter, a increases by one unit in every time-step up to the maximum value A . The young will become independent on day $t + A$, i.e. a parent always terminates care at the start of day $t + A$ if it has not done so already. An animal which cares for its young until then can begin searching for another mate at the start of day $t + A + 1$, with $a(t + A + 1) = 0$. We assume that the animal's mate does not react to the focal parent's behaviour and alter the rewards for care or desertion. For example, either the mate plays no part in parental care or the mate continues to care regardless of the behaviour of the focal individual.

Every day, animals have two possible choices of action: adults without dependent offspring may either forage or search for a mate, while parents may either desert or continue to care for their young. An animal that is foraging finds food items each day with a probability of unity. If a foraging animal has energy reserves x at the beginning of day t , then its reserves at the beginning of day $t + 1$ are $x + x_f$, where x_f is the net energetic content of the items which are eaten (having subtracted the energetic costs of foraging). If an animal with energy reserves x is searching for a mate, then it finds one with probability P_r and immediately produces offspring, incurring an energetic cost x_1 , so that its energy reserves fall to $x - x_1$. For a female, this cost of offspring production might be the cost of laying a clutch; for a male, it could be the cost of territorial defence or nest building. If it is unsuccessful at finding a mate (with probability $1 - P_r$), then its reserves remain constant, on average. Parents which continue to care for their young incur an energetic cost x_c during each day of caring. A parent that deserts its offspring pays no energetic cost, on average. All of these changes in energy reserves are stochastic: each change has a mean value (say

Figure 1. The combined effect of age and seasonal dependence on the value of deserted broods. $B(a, t)$ is the value of a brood of age a which is deserted at time t .

m), which occurs with a probability of $\frac{1}{2}$ and changes of size $m \pm 1$ occur, each with a probability of $\frac{1}{4}$.

An animal receives an increment to its reproductive success, $B(a, t)$, for each set of offspring which it raises during the season. This reward depends on the time t in the season at which the offspring are deserted and the age a of the offspring when they are deserted (see figure 1). We assume that this reward is the product of two factors. The first factor depends on the age of the offspring and is given by a function $M(a)$ which represents, for example, an increased predation risk for the offspring in the absence of the focal parent. The value of the offspring is also adjusted by a seasonal factor, $V(t_A)$, depending on the time t_A at which the young reach independence (age A). This factor is introduced to allow for the fact that offspring that reach independence late in the season may be worth less than those that do so earlier. This could, for example, be used to express the fact that the offspring of migratory birds must fledge before migration if they are to survive the journey. Combining these two factors, the reproductive value of a brood or clutch which is deserted at time t and age a is taken to be

$$B(a, t) = M(a)V(t + A - a). \quad (2.1)$$

For the results discussed in § 3, the following functions were selected

$$M(a) = \frac{A^k + H^k}{A^k} \left(\frac{a^k}{a^k + H^k} \right) \quad (2.2)$$

and

$$V(t_A) = \begin{cases} \left(1 + \left(1 - \frac{\theta}{T} \right)^n \right) \left(\frac{(T - t_A)^n}{(T - t_A)^n + (T - \theta)^n} \right), & \text{when } 0 \leq t_A < T \\ 0, & \text{when } t_A \geq T \end{cases} \quad (2.3)$$

The overall shape of the brood value $B(a, t)$ is controlled by the four parameters H , k , θ and n . By varying these parameters a variety of biological situations may be modelled. By changing the values of H and k , offspring which are precocial, semi-precocial or altricial may be considered. Low values of θ and n produce a gradual reduction in offspring value over a season (for example,

because of a decline in the quality of food items), whereas high values of θ and n produce a sharp cut-off in brood value towards the end of the breeding season (for example, because of a time-limit introduced by the need to migrate). The shape of the brood value function for one set of parameter values is illustrated in figure 1.

In addition to the reproductive success accruing from any offspring raised during the season, an animal receives a state-dependent reward for survival to the end of the season. This is a schematic representation of the value of all future breeding seasons. If the energy reserves of the animal at time T are x (i.e. $X(T) = x$), then the animal obtains a reward

$$R(x) = S \frac{1 - \exp(-x/X_{\max})}{1 - \exp(-1)}. \quad (2.4)$$

The reward increases with increasing reserves so that we are assuming, for example, that higher reserves at the end of the season translate into a greater probability of surviving until the next breeding season. The function $R(x)$ is decelerating so that the value of an extra unit of reserves decreases as the level of reserves increases. The constant S is a scaling factor. The case $S = 0$ could apply to the case of an animal in its final breeding season.

In this model a strategy is a rule specifying how the behaviour of the adult depends on its energy reserves, x , the age of its offspring, a , and the time, t . For parents the options are either to 'desert' or to 'continue care'; for adults without dependent offspring the options are either 'feed' or 'search for a mate'. The optimal strategy for an animal is that which maximizes its expected reproductive success, including both the rewards for survival (i.e. future breeding seasons) and for offspring produced in the current season. This strategy is determined by using the dynamic programming technique of working backwards from the final time T (Houston *et al.* 1988; Mangel & Clark 1988; Houston & McNamara 1999; Clark & Mangel 2000). The dynamic programming equations are cited in Appendix A. In § 3 we describe the optimal strategy for an individual and discuss its dependence upon the various parameters in the model.

3. OPTIMAL STRATEGIES

The set of parameter values shown in table 1 is used as a baseline case, and we only mention the values of parameters explicitly when they differ from the values given there. First, we describe the optimal strategy for these baseline values. We then examine the effects of changing the various costs and benefits of care. For example, we can change the benefit of continuing care by altering the shape of the offspring value function $B(a, t)$. The costs of care can be altered by changing the probability of remaining, P_r , and the breeding success in future seasons, S . We also look at the effects of changing the energetic costs of caring, the energetic costs of offspring production and the availability of food.

(a) Baseline case

The optimal strategy for adults without dependent offspring is to search for a mate when energy reserves are high and to concentrate on feeding when reserves are low

Table 1. Parameters for the dynamic programming model of parental care decisions.

parameter	symbol	baseline value	variation
final time	T	40	fixed
maximum energy reserves	$X_{\max}$	25	fixed
maximum brood age	A	10	fixed
parameter for function describing deserted brood value	k	5	fixed
parameter for function describing deserted brood value	θ	35	fixed
parameter for function describing deserted brood value	n	3	fixed
parameter for function describing deserted brood value	H	5	2–8
maximum reward for survival to T	S	1	0–5
remating probability	P_r	0.10	0.05–0.20
mean energetic value of food items	x_f	2	1–3
mean energetic cost of care	x_c	1	0–2
mean energetic cost of laying	x_l	3	3–7

(see figure 2a). As the season progresses, animals switch from feeding to searching at lower levels of reserves in order to obtain offspring which will become independent before the end of the season. However, towards the end of the season, the optimal strategy becomes modified by the trade-off between breeding success in current and future seasons. As the value of offspring is decreasing as the season progresses it becomes more advantageous for an adult to increase its own energy reserves, thus improving its prospects for future breeding seasons. Animals switch from feeding to searching for a mate at progressively higher levels of reserves and, eventually, stop searching altogether (figure 2a).

The optimal desertion decision of a parent depends on both the age of its young and the time within the breeding season. Early in the season, a parent deserts young offspring only when its energy reserves are so low that it risks starvation (figure 2b). For example, with the baseline parameters shown in table 1, a parent with three units of reserves will starve with a probability of 1/16 if it continues to care for one more day. Such a parent, therefore, deserts its offspring. While avoidance of starvation is commonly cited as a reason for desertion, the optimal policy shows that desertion can be induced by a threat of starvation that is not immediate. A parent with four units of reserves could care for at least one more day without incurring any risk of starvation. After that day of care, the parent's reserves are reduced (on average) to three units and the adult would then desert. However, very young broods, which are attended for only one more day, are not very valuable and the time spent on care could be more profitably used in feeding, thereby hastening remating and the production of a further brood. The animal, therefore, deserts its offspring. Even though the risk of starvation is not immediate, we will refer to all desertion at low levels of reserves as 'desertion to avoid starvation'. Towards the end of the season, the optimal strategy is modified by the existence of future breeding seasons and young offspring are deserted at progressively higher levels of reserves.

Throughout the season, older offspring may be deserted whatever the level of the parent's energy reserves (figure 2c). Since adults with high energy reserves could

continue to care for their young until they reach independence without incurring any risk of starvation, it is clear that not all parents are deserting to avoid starvation: some must be deserting in order to remate and raise more young. This can be confirmed by looking at the region $20 \leq t \leq 24$ in figure 2c. At this point, a parent deserts its offspring to avoid starvation if its reserves are low, and to remate if its reserves are high. For intermediate levels of reserves it continues to care. This result indicates that the relationship between the state of parents (such as energy reserves) and desertion behaviour may not be as simple as 'care above a critical level of reserves and desert below'.

Combining the optimal strategies for animals with (figure 2c) and without (figure 2a) dependent offspring, we can determine the behaviour of an adult immediately after it deserts (figure 3). In figure 3, animals with reserves greater than four would not incur any risk of starvation if they cared for their offspring until independence (two more days), so we can see that some animals which are deserting in order to remate do not immediately begin searching for a new mate. Instead, they begin by spending some time feeding to build up their levels of reserves to ensure that any future offspring can be successfully reared. This means that it may not be possible to infer the reason for desertion by observing an animal's behaviour immediately afterwards.

(b) *Altering the costs and benefits of care*

When future breeding seasons do not exist ($S = 0$), the optimal strategy is changed in two ways. (i) Individuals without dependent offspring continue to search for a mate until the end of the season. (ii) A late-season parent will continue to care for offspring until they become independent or until the parent dies. In contrast, increasing the value of future breeding seasons ($S > 1$) has little effect on the optimal strategy.

The energetic costs associated with raising offspring can be divided into two types: costs of care (x_c) which are paid for every time-step that care is continued, and costs of offspring production (x_l) which are paid only once for each set of offspring. Increasing the energetic cost of caring (x_c) changes the optimal strategy in two ways. (i) As the cost

Figure 2. (a) The optimal strategy for animals without dependent offspring. These animals forage when their reserves lie in the shaded area and search for a mate when their reserves lie in the unshaded area. (b) The optimal strategy for parents with young offspring ($a = 1$). Parents desert when their reserves lie in the shaded area and care when their reserves lie in the unshaded area. (c) The optimal strategy for parents with older offspring ($a = 8$). Parents desert when their reserves lie in the shaded area and care when their reserves lie in the unshaded area.

of care increases, the critical level of reserves below which a parent deserts is raised. (ii) The behaviour of adults without dependent offspring is changed: they only search for a mate at higher levels of reserves (figure 4). This means that they begin a period of care with higher reserves than they would if the cost of care were lower. Increasing

Figure 3. Behaviour of animals immediately after deserting a brood of age $a = 8$. Animals forage after desertion if their reserves lie in the diagonally shaded area, while they immediately begin searching for a new mate if their reserves lie in the cross hatched area. In the unshaded area animals have not deserted their brood.

Figure 4. The optimal strategy of animals without dependent offspring for different energetic costs of care, x_c . The solid line shows the boundary between the foraging and searching regions (see figure 2a) for $x_c = 1$. The dotted line shows the same boundary for $x_c = 2$.

the cost of offspring production (x_1) also causes adults without dependent young to increase their energy reserves to a higher level before embarking on the search for a new mate. However, increasing x_1 from three to seven produces a change in the optimal action for parents at only a few combinations of reserves, brood age and time in the season.

Increasing the mean value of food items x_f changes the optimal strategy for adults without dependent offspring (figure 5a). Since animals need to spend less time foraging before their reserves reach any given level, they begin to search for a mate at slightly higher levels of reserves and begin building up their reserves for survival to the next breeding season slightly later. Increasing the gain rate whilst foraging also affects parental care behaviour: parents will continue to desert in order to remate until later in the season; and they delay desertion induced by the need to build up their reserves for future seasons (figure 5b).

Figure 5. The optimal strategy for different values, x_p , of food items. (a) The optimal strategy for animals without dependent offspring: the solid line shows the boundary between the foraging and searching regions (see figure 2c) for $x_f = 2$. The dotted line shows the same boundary for $x_f = 1$. (b) The optimal strategy for birds with a brood of age $a = 8$: the solid line shows the boundary between the caring and deserting regions (see figure 2b) for $x_f = 2$. The dotted line shows the same boundary for $x_f = 1$.

Decreasing the daily remating probability has little effect on the behaviour of animals without dependent offspring, but it does increase the age at which offspring are deserted because the parent is attempting to remate. This age is $a = 7$ for the baseline parameter values and $a = 8$ for $P_r = 0.05$.

By changing the value of the parameter H , the benefits of continued care to a given age can be altered. A lower value of H means that deserted offspring are more valuable at a given age of desertion, whereas a higher value of H means that the offspring are correspondingly less valuable. Low values of H could be interpreted as representing precocial offspring, which are well able to fend for themselves, whereas high values of H could represent altricial offspring which would not survive in the absence of an extended period of care. Low values of H lead to an optimal strategy in which parents desert their offspring in order to remate when their offspring are younger. For example, with $H = 2$ desertion for remating occurs at age $a = 4$ compared to $a = 7$ in the baseline case. Conversely, with $H = 8$ desertion in order to remate does not occur, but desertion to avoid starvation occurs at much higher

levels of reserves because parents would have to care for much longer in order to reap the benefit of raising offspring. The optimal strategy of adults without dependent offspring is also altered by changing the benefit of continued care: the level of energy reserves at which animals switch from feeding to searching increases with increasing H .

4. POPULATION BEHAVIOUR

In a simple optimization model all individuals are assumed to be identical. This means that the optimal individual behaviour predicts what will be observed when the population is studied (for example, average duration of care). In contrast, since individuals can differ in their energy reserves, the derivation of population level predictions from our model is much less direct.

Once the optimal action for an animal with a particular level of energy reserves has been established, we can determine the probability that the animal's energy reserves will be at any other level after performing that action. By specifying the distribution of energy reserves in a population at the beginning of the breeding season, $p(x, a, t) = 0$, we can use the optimal strategy to determine the distribution of animals in each state at time $t = 1$, $p(x, a, 1)$. From this distribution we can find the distribution of states at time $t = 2$, $p(x, a, 2)$, and so on up to the end of the breeding season $t = T$. Once the distribution of states, $p(x, a, t)$, is known for all times in the breeding season, this information can be combined with the optimal strategy to determine aggregate behaviours in that population, such as the distribution of the number of breeding attempts, the probability of offspring desertion and the average age of offspring which are deserted. For the results discussed in § 5 we have assumed that all animals are without dependent offspring at the beginning of the breeding season. At this time, their reserves are uniformly distributed over the top five values ($X_{\max} - 4 \leq x \leq X_{\max}$), so that they are ready to begin searching for a mate and producing offspring.

(a) Number of breeding attempts

The optimal strategy of care and desertion determines the number of broods or litters that an animal produces during the breeding season. This number is variable for two reasons. (i) Because of stochasticity, individuals differ in their energetic costs for offspring production and care and in their success at finding mates. (ii) Individuals differ in the level of reserves with which they begin the breeding season. For the baseline parameter values in table 1, ca. 4%, 37%, 56.5%, and 2.5% of animals have 0, 1, 2, and 3 sets of offspring, respectively. The mean number of breeding attempts during the season is 1.57. The effect of changing various parameter values is summarized in table 2.

(b) Average duration of parental care

The probability $\delta(a, t_0)$ that offspring produced at time t_0 will be deserted at age a is

Table 2. The effect of changing parameters on the mean number of breeding attempts ($\bar{B}$) and the proportion of adults dying as a result of parental care decisions (D).

parameters	$\bar{B}$	D
baseline	1.57	0.3%
$S = 0$	1.42	27.0%
$S = 5$	1.55	< 0.1%
$P_r = 0.05$	1.03	0.1%
$P_r = 0.20$	2.16	0.5%
$x_c = 0$	1.72	< 0.1%
$x_c = 2$	1.45	0.4%
$x_1 = 5$	1.50	0.3%
$x_1 = 7$	1.44	0.4%
$x_f = 1$	1.45	0.4%
$x_f = 3$	1.67	0.3%
$H = 2$	2.07	0.2%
$H = 8$	1.44	0.4%

$$\delta(a, t_0) = \frac{\sum_{x=1}^{x_{\max}} p(x, a, t_0 + a) I_D(x, a, t_0 + a)}{\sum_{x=1}^{x_{\max}} p(x, 1, t_0)}, \quad (4.1)$$

where $\sum p(x, 1, t_0)$ is the proportion of the population which produces offspring on day t_0 , and $I_D(x, a, t)$ is the indicator function taking the value unity if the optimal action for the specified a and t is to desert and being zero otherwise. The average age at which offspring produced at time t_0 are deserted is

$$\bar{a}_d(t_0) = \sum_{a=1}^A a \delta(a, t_0). \quad (4.2)$$

Conversely, to calculate the average duration of care for such broods, we need to include the probability that parents will die from starvation during care. Therefore, the average duration of care is:

$$\bar{a}_c(t_0) = \sum_{a=1}^A a \Delta(a, t_0), \quad (4.3)$$

where

$$\Delta(a, t_0) = \frac{\sum_{x=1}^{x_{\max}} p(x, a, t_0 + a) I_D(x, a, t_0 + a) + p(0, a, t_0 + a)}{\sum_{x=1}^{x_{\max}} p(x, 1, t_0)}. \quad (4.4)$$

In equation (4.4), $p(0, a, t_0 + a)$ is the proportion of adults that die of starvation on day $t_0 + a$ while attempting to care for offspring of age a . Apart from the case when there is no future breeding season ($S = 0$), the number of animals that die during the season as a result of their parental care decisions is typically less than 1% of the population (see table 2). Consequently, the difference between

Figure 6. The average duration of care for broods initiated on each day of the season for different values of the reward for adult survival: $S = 0$ (squares), 1 (triangles) and 5 (crosses). Note that no offspring are produced after $t_0 = 29$ because they would have a value of zero by equation (2.3).

Table 3. The effect of increasing parameters on the average duration of care for early, mid- and late-season broods. A plus sign represents an increase and a minus sign represents a decrease.

parameter	average duration of care		
	early	middle	late
H	+	+	+
S	—	+	—
P_r	—	—	—
x_c	—	+	—
x_1	—	+	—
x_f	+	—	+

the average age of desertion and the average duration of care is usually negligible.

For most of the parameter values we have considered, the average duration of care is about 8 days for offspring produced at the beginning of the breeding season (figure 6). In the middle of the season there is, typically, a reduction in the duration of care to around 7 days followed by an increase to about 9 days. This is due to the region in the strategy for parents with older broods (figure 2c) where it is optimal to continue care at intermediate levels of reserves. There is then a gradual reduction in the average duration of care to about 3 days. One exception to this pattern is the case when there is no future breeding season ($S = 0$). In this case, at the end of the season, parents attempt to continue care until the offspring reach independence ($a = 10$). However, the average duration of care is less than 10 days because some parents die during the period of care. The effect of changing costs or benefits of care and desertion is summarized in table 3.

A lower value of H means that deserted offspring are more valuable at a given age of desertion, and this leads to a decrease in the average duration of care as H decreases. For $H = 8$ the average duration of care is just less than 10 days throughout the majority of the breeding

Figure 7. The average duration of care for broods initiated on each day of the season for different costs of laying: $x_1 = 3$ (squares), 5 (triangles) and 7 (crosses).

season, whereas for $H = 2$ the average duration of care is about 4 days. When future breeding seasons exist ($S > 0$), there is a decline in the average duration of care for offspring produced late in the season whatever the value of H .

Increasing the remating probability P_r reduces the average duration of care, as might be expected. However, changing the remating probability has an effect on the average duration of care even late in the season when no further offspring will be raised ($t > 25$). This occurs because, although the optimal strategies for $t > 25$ are unchanged, a higher remating probability means that, on average, more breeding attempts have already been undertaken and consequently parents' average levels of reserves are lower when they begin care.

Increasing the energetic cost of offspring production produces opposing effects depending on the time in the breeding season (figure 7). Early in the season, increasing the cost of offspring production decreases the average duration of care. For breeding attempts which are initiated between $t = 10$ and $t = 15$, increasing the cost of offspring production increases the duration of care. This is because an increased cost of offspring production means that more parents are present in the 'caring window' at intermediate levels of reserves during the mid-season. For breeding attempts initiated later in the season, increasing the cost of offspring production decreases the duration of care. The effect of changing the cost of offspring production is quite small because adults without dependent young alter their behaviour to compensate for the change in the costs they will incur when caring for offspring.

Increasing x_c or x_f also produces an oscillating change in the average duration of care as summarized in table 3.

5. DISCUSSION

We have considered parental care and the desertion of offspring within a life-history framework, involving trade-offs between current and future reproduction. We have constructed a dynamic optimization model of parental care behaviour, which allows a parent to reproduce several times within a season and to trade off the value of these breeding attempts against a terminal reward representing the value of future breeding seasons. Our model is differ-

ent from previous dynamic models of parental care (Sargent 1990; Kelly & Kennedy 1993). Sargent (1990) modelled the parental care behaviour of fishes, assuming that several behaviours (such as feeding, mating and caring) are carried out simultaneously, but this assumption is unrealistic for many animals such as birds or mammals. Kelly & Kennedy (1993) used a dynamic programming approach to model the parental care behaviour of female Cooper's hawks (*Accipiter cooperii*). Their model does not allow deserting females to remate, since such behaviour was not observed in the natural population. In addition, although their model is time-dependent, time-periods are defined in terms of brood age. Our model treats brood age and time within the season as separate variables.

Desertion of young is a common feature among many birds and mammals, and researchers often surmise that low food levels induce this behaviour (Clutton-Brock 1991; Monaghan *et al.* 1992; Kelly & Kennedy 1993; Chaurand & Weimerskirch 1994; Olsson 1997; Tveraa *et al.* 1997). The model supports this assumption, but it shows that desertion may result from the threat of future starvation. The model also predicts that animals should desert their offspring when they have a significant chance of remating. This prediction is consistent with the behaviour of various fishes and birds. Male fishes are likely to desert their broods when the OSR is female-biased (Keenleyside 1983; Keenleyside *et al.* 1990; Balshine-Earn 1995) and female rock sparrows (*Petronia petronia*) desert when the adult sex ratio is male-biased (Pilastro *et al.* 2001). Also, Burley (1988) and Møller (1994) have shown that attractive males provided less care than unattractive ones in zebra finches (*Poephila guttata*) and barn swallows (*Hirundo rustica*), respectively. Finally, the model predicts that the capability of the young to survive on their own should influence the probability of desertion. This prediction is consistent with the deserting behaviour of sticklebacks and birds. MacDonald *et al.* (1995) found that male sticklebacks deserted their embryos more often in environments where they have a high chance of survival when unattended. Sillén-Tullberg & Temrin (1994) compared the parental care patterns of altricial and precocial birds and found that one parent terminates parental care in precocial birds more often than in altricial ones.

The model also illustrates the diversity of reasons for desertion that may occur within a single population. Snyder *et al.* (1989) reported that snail kites (*Rostrhamus sociabilis*) terminated incubation when the marsh dried out and the parents were presumably food-stressed. Parents may also desert when they have high reserves and a reasonable chance of remating. For example, snail kites may also desert their brood and existing mate if snails are very abundant (Beissinger & Snyder 1987). In the latter situation one parent was able to raise the young to independence without the help of its mate. Our model also shows that the cause of desertion cannot always be determined from observations of an animal's behaviour immediately after it leaves its offspring.

In the model the number of breeding attempts is only partly determined by the optimal strategy of care and desertion. Different individuals may make different numbers of attempts within a season due to differences in their state (reserves) at the beginning of the season and due to

individual good or bad luck in foraging or finding mates. This results in a distribution in both the duration of care and the number of breeding attempts within a season. The model also shows that the duration of care for each breeding attempt may vary with the time in a season. When there are no future breeding seasons, the lengths of care follow the pattern that early in the season parents care for offspring for a shorter time than they care for offspring which are produced later. However, this pattern changes when future breeding seasons exist: offspring produced late in the season are given a shorter period of care than those produced earlier. This occurs because a parent cares until its reserves fall below a level that is determined by the trade-off between the survival of those offspring and the expected reproductive value of the adult at the end of the season.

The average duration of care is predicted to change in a non-monotonic way over the season (see figures 6 and 7). The model also predicts changes in the average duration of care at any given time during the season in response to changes in foraging conditions, costs of care, or the availability of mates. An increase in the rate at which new mates are found leads to a decrease in the duration of care throughout the season. On the other hand, changes in an energetic factor (daily cost of care, cost of laying or foraging conditions) can lead to an increase or a decrease in the duration of care depending on the time in the season (see table 3). Interestingly, although an increase in the availability of mates, and an improvement in foraging conditions, both act to reduce the (expected) time between broods, they produce opposing effects on the duration of care for most of the breeding season. This is due to the link between the duration of care and the time spent foraging between broods, which is illustrated in figure 5. An increase in the daily energetic costs of care leads to a decrease in the duration of care.

The model also shows that the conditions prevailing for parents can affect the choices made by adults without dependent offspring. For example, adults without dependent young may increase the time between breeding attempts which they spend foraging in order to compensate to some extent for increases in the cost of raising future offspring. Similarly, the conditions prevailing for animals without young can affect parental care behaviour. For example, changing the value of food items that an animal finds whilst foraging alters the optimal strategy of parents. The model also shows that changing some of the energetic costs of offspring production can have different consequences at different times in the breeding season. For example, increasing the cost of offspring production may either increase or decrease the probability of desertion. This suggests that future studies of offspring desertion should take into account that parents may respond differently to experimentally induced costs (such as the cost of egg laying) depending on the time in the breeding season.

We have focused on ecological factors influencing parental care. Our model shows that desertion is a sophisticated process, even when only a single animal is considered explicitly. Incorporating interactions between animals into ecologically more realistic models will be challenging.

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APPENDIX A: THE DYNAMIC PROGRAMMING EQUATIONS

Let $V(x, a, t)$ be the reproductive value of an animal if it has offspring of age a and energy reserves at level x at time t . The reproductive values at time t can be deduced from the reproductive values at time $t + 1$ in the following way.

When the animal has no dependent offspring (i.e. $a = 0$) it can choose between feeding and searching for a mate. If it feeds, then its reserves increase by an amount $x_t + z_i$ with probability p_i , where $\{z_1, z_2, z_3\} = \{-1, 0, +1\}$ and $\{p_1, p_2, p_3\} = \{0.25, 0.5, 0.25\}$. Thus, an animal with reserves x at time t which chooses to feed has reproductive value

$$H_f(x, t) = \sum_{i=1}^3 p_i V(x + x_t + z_i, 0, t + 1). \quad (\text{A } 1)$$

An animal which searches for a mate finds one with probability P_r . If it finds a mate it produces some offspring which have the lowest age, $a = 1$, and its reserves decrease by an amount $x_1 + z_i$ with probability p_i , where z_i and p_i have the same values as above. If it fails to find a mate then its reserves change by an amount z_i with probability p_i . So, an animal with reserves x at time t which chooses to search has reproductive value

$$H_s(x, t) = P_r \sum_{i=1}^3 p_i V(x - x_1 - z_i, 1, t + 1) + (1 - P_r) \sum_{i=1}^3 p_i V(x + z_i, 0, t + 1). \quad (\text{A } 2)$$

It is optimal to search for a mate if $H_s(x, t) > H_f(x, t)$, and it is optimal to feed if $H_f(x, t) \geq H_s(x, t)$.

An animal with dependent offspring (i.e. $a \geq 1$) can choose either to continue to care for the young or to desert them. If it cares, the offspring become one day older ($a \rightarrow a + 1$) and the parent's reserves decrease by $x_c + z_i$ with probability p_i . So a parent with offspring of age a and energy reserves at level x at time t which chooses to continue care has reproductive value

$$H_c(x, a, t) = \sum_{i=1}^3 p_i V(x - x_c - z_i, a + 1, t + 1). \quad (\text{A } 3)$$

If the parent deserts a brood of age a at time t , then the brood has value $B(a, t)$ to the parent. The form of this function is given in equation (2.1). The reserves of an adult which deserts at time t change by an amount z_i by time $t + 1$ with probability p_i . This adult has no dependent offspring at time $t + 1$ (i.e. $a = 0$). Therefore, a parent which decides to desert its offspring has reproductive value

$$H_d(x, a, t) = B(a, t) + \sum_{i=1}^3 p_i V(x + z_i, 0, t + 1). \quad (\text{A } 4)$$

It is optimal to care for offspring if $H_c(x, a, t) > H_d(x, a, t)$, and it is optimal to desert if $H_d(x, a, t) \geq H_c(x, a, t)$. The process of finding the reproductive values at time t from those at time $t + 1$ is begun by using the terminal reward condition

$$V(x, a, T) = R(x), \quad (\text{A } 5)$$

where $R(x)$ is given by equation (2.4).

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