

The role of mortality risk in parental behaviour

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ABSTRACT

Background: A parent feeding its young during the breeding season faces a trade-off between mortality risk and provisioning young with food for growth.

Question: How should the parent behave to maximize reproductive success when mortality to both parent and young are considered?

Mathematical method: Using an optimality model, we establish new formulae to describe parental behaviour when there is a trade-off between growth rate of the young and mortality risk to both parent and young.

Key assumptions: We consider mortality functions for both parent and young. These comprise the sum of a background mortality risk and a mortality risk attributed to parental behaviour.

Conclusions: Mortality is an important parameter in the determination of parental behaviour. As the dependence of the mortality of the young on parental effort grows, a parent should invest a greater proportion of time in being vigilant for predators. An increase in other mortality parameters prompts the opposite effect. Mortality should be described by multiple parameters to predict fully how a parent should behave.

Keywords: growth rate, mortality risk, optimality model, parental care.

INTRODUCTION

Parenting is a multivariate trait (Clutton-Brock, 1991; Barta *et al.*, 2014). Parents must decide how to allocate resources to different and often competing activities – for example, foraging for energy for young can be incompatible with protecting them from predators (Elgar, 1989; Lima, 1990).

When making behavioural decisions, animals are known to consider both the rate of energy gain and predation risk (e.g. Werner *et al.*, 1983; Bednekoff and Krebs, 1995; Kotler, 1997; MacLeod *et al.*, 2005; Quinn *et al.*, 2012; Bonter *et al.*, 2013). Great Skua (*Catharacta skua*) parents under pressure to meet their young's energy demands increase their foraging effort but are still constrained by the need to minimize the frequency with which chicks are left unattended and vulnerable to predation (Caldow and Furness, 2000).

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For most birds, nest predation is the primary cause of offspring mortality (Ricklefs, 1969). In response to predation risk, incubating parents exhibit adaptive changes in behaviour to reduce the probability of predation (Skutch, 1949; Lima, 1987; Montgomerie and Weatherhead, 1988; Lima and Dill, 1990; Martin, 1992). Birds with a higher nest predation risk are expected to exhibit faster growth to minimize exposure time to predators (Williams, 1966; Lack, 1968; Martin, 1995; Remeš and Martin, 2002). However, this might not always be the case. Increased predation risk can lower the rate of nest visits by parents to reduce the risk of predators discovering the location of the nest and young (Skutch, 1949; Eggers *et al.*, 2005; Fontaine and Martin, 2006). Greater predation risk can cause reduced growth rates of young (Thomson *et al.*, 2006) via a reduced rate of food delivery (Scheuerlein and Gwinner, 2006).

A trade-off exists for an animal if, to achieve a high rate of energy gain, it must accept the cost of a high rate of predation. The energy–predation trade-off has been studied widely both empirically (Sih, 1987; Lima and Dill, 1990; Lima, 1998) and theoretically (Abrams, 1982; Gilliam, 1982; Pulliam *et al.*, 1982; Gilliam and Fraser, 1987; Brown, 1988; Ludwig and Rowe, 1990; Houston *et al.*, 1993; Houston and McNamara, 1999). A central concept of the energy–predation trade-off is that an animal can control its rate of energetic intake and its risk of being killed by a predator through its behaviour (Abrams, 1982; Houston and McNamara, 1989; Houston *et al.*, 1993; McNamara and Houston, 1994). The energy–predation trade-off is often analysed in terms of the optimal behaviour of an animal, either given a discrete or continuous range of behaviours (Houston *et al.*, 1993). Implicit in all of these models is the marginal rate of substitution (Caraco, 1979), which characterizes the energy–predation trade-off by comparing the benefit of gaining energy with the cost of mortality.

There have been previous attempts at state-dependent models of the energy–predation trade-off (Gilliam, 1982; Mangel and Clark, 1986; Houston and McNamara, 1989; Houston *et al.*, 1993; McNamara *et al.*, 2009). Gilliam (1982) considered an animal that had to grow to a critical size before it could reproduce, independent of the time of reproduction. He showed that an animal should choose habitats that minimize the ratio of mortality rate to growth rate. Houston and McNamara (1989) provide a more general expression than Gilliam (1982), finding the optimal strategy that maximizes the rate of change of reproductive value in an environment characterized by intake rate and mortality rate.

All of the above research looked at the effect of mortality on a forager itself. It is known that parent birds face increased vulnerability to predation attributed to parental care (e.g. Ainley and DeMaster, 1980), as do their young (Skutch, 1949; Snow, 1962). Here, we extend the energy–predation trade-off to include parents feeding their young with two sources of mortality. We analyse explicitly the trade-off a parent faces between the mortality of itself and its young and the growth rate of its young. We are interested in the optimal decision from the point of view of the parent given the state of its young.

We derive a general expression in which reproductive value is dependent on both state and time as well as a case where, like Gilliam (1982), the parent's reproductive success is dependent on state. Gilliam uses the idea that a forager increases its state to achieve a critical level. We use this idea in the context of a parent feeding its young and assume the young must reach a critical size to achieve independence. The analysis for our model is more general than those of both Gilliam (1982) and Houston and McNamara (1989) and includes these as special cases.

A limitation of previous theoretical studies of the energy–predation trade-off is that predation risk in the context of parents feeding their young is described as one overall effect (Clark and Ydenberg, 1990; Ghalambor *et al.*, 2013; Royle *et al.*, 2014). Royle *et al.* (2014) illustrate that the

allocation of resources to two competing parenting demands – nest defence and provisioning rate – is sensitive to environmental factors. An increase in nest predation risk induces a plastic response in which more time is spent by the parent on nest defence versus provisioning. Although mortality risk is addressed, it is not obvious when a parent would switch from a safe to a more risky option with a change in predation risk.

Clark and Ydenberg (1990) predict that a parent should spend a greater proportion of time defending their young as the young grow older and become more valuable. They consider a parent that essentially makes a single decision about when to stop feeding its young. Unlike Clark and Ydenberg (1990), the decision of the parent in our model is characterized by how much the parent should feed its young to ensure the young reach a critical size for independence. Furthermore, whilst Clark and Ydenberg consider a fixed mortality for both the parent and its young, we consider mortality functions for both parent and young that are dependent on the parent's behaviour.

Other models have also considered sources of mortality for both parent and dependent young. Dall and Boyd (2002) consider mortality to both the parent and young mediated by the allocation of energy to the parent and young. Mortality is considered through the eventual possibility of starvation rather than immediate mortality risk. Unlike Dall and Boyd, our model considers a direct mortality trade-off. We show that mortality risk cannot be described by one parameter alone. We do this by investigating the effect on parental feeding behaviour when mortality of both the parent and its dependent young are taken into consideration. We describe mortality by four effects: for both parent and young there is a background mortality risk that is independent of parental behaviour and mortality risk arising from the provisioning rate of the parent. We illustrate this with an optimization model. We determine the proportion of time a parent should spend foraging for energy for their young as opposed to being vigilant given the mortality to both itself and its young. We develop a general approach that extends the models of Gilliam (1982) and Houston and McNamara (1989). We also specify how mortality risk and growth are dependent on the size of the young and illustrate the trade-off a parent faces between minimizing mortality risk to itself and mortality risk to its young.

MODEL

Consider an avian parent and its dependent young during the nestling stage of reproduction. For simplicity we treat both parents as one acting parent and the conflict between parent and young is disregarded. Mortality to the young is associated with nest predation and if one dies, then all die. For definiteness we take the state of the young to be their size x . Young must reach the critical size x_{max} to achieve independence. Young that do not reach x_{max} do not survive. If a parent is killed before its young reach independence, the young also die. We are interested in the optimal decision from the point of view of the parent. The parent is attempting to maximize its expected lifetime reproductive success, i.e. the expected number of its offspring that survive to reproductive maturity over its lifetime. If the young reach independence at size x_{max} , then R of these young survive to reproductive maturity. Here R could potentially depend on the time that young reach x_{max} , although we take R to be a constant in our illustrative examples. Once the young become independent, the expected future reproductive success of the parent is r , i.e. the mean number of future offspring reaching reproductive maturity. In our model, we assume that the death of the young means a loss of the parent's current reproductive potential but it does not affect the

parent's future success, which is again r . For simplicity, r is taken as a constant. This might be a reasonable assumption if there is just one breeding attempt per year and the probability of surviving to breed next year does not depend on the time at which care ceases in the current year.

The strategy of the parent is the function $\gamma(x)$ that specifies the growth rate for the young at each size x . Parental self-feeding is implicitly included in our model (see evolutionary-ecology.com/data/3134Appendix.pdf, section 4). Here, however, we will only be concerned with the foraging effort of the parent for its young on top of self-feeding. We define $M_p(\gamma) > 0$ and $M_y(\gamma) > 0$ to be the mortality rates of the parent and young, respectively. Both mortality rates are increasing functions of the current growth rate of the young. We are interested in the instantaneous decision of the parent given the size of the young and that the parent behaves optimally. By natural selection we expect a parent to maximize expected lifetime reproductive success. We denote the optimal growth rate of the young when the young is size x by $\gamma^*(x)$. $M_p(\gamma^*)$ and $M_y(\gamma^*)$ are the resulting mortality functions.

ANALYSIS

In our analysis, we define the reproductive value of a parent at a given time to be the expected number of offspring that survive to reproductive maturity from any current brood and all future broods. Reproductive value depends on state, time, and future behaviour. We let $V(x, t)$ denote the reproductive value of a parent with young of size x at time t , given that the parent behaves optimally during care. By assumption we have $V(x_{\max}, t) = R + r$. We give a heuristic derivation of the Hamilton-Jacobi-Bellman equation of control theory (Jacobs, 1974) for V during the period of care. Consider a parent with young of size x at time t , where $x < x_{\max}$. If the parent behaves to achieve growth rate γ between t and $t + \delta$, where δ is small, the probabilities of death of the parent and young between time t and $t + \delta$ are $\delta M_p(\gamma)$ and $\delta M_y(\gamma)$, respectively (to first order in δ). If both the parent and young are alive at time $t + \delta$, the size of the young is $x + \gamma\delta$. Thus if the parent behaves optimally from time $t + \delta$ onwards, its reproductive value is

$$W(x, t; \gamma) = V(x + \gamma\delta, t + \delta)[1 - \delta M_p(\gamma) - \delta M_y(\gamma)] + r\delta M_y(\gamma) + o(\delta), \quad (1)$$

where $o(\delta)$ represents higher-order terms. The first term on the right-hand side of expression (1) is the product of the reproductive value of the parent at time $t + \delta$ given it and the young survive until this time and the probability of both the parent and young surviving. The second term is the product of the reproductive value if the young die and the probability the young die between t and $t + \delta$. Of course, the reproductive value of the parent is 0 if it dies, since the young also die.

We exploit the fact that V is smooth by approximating the term $V(x + \gamma\delta, t + \delta)$ using the Taylor expansion to give the equation

$$V(x + \gamma\delta, t + \delta) = V(x, t) + \gamma\delta \frac{\partial V}{\partial x} + \delta \frac{\partial V}{\partial t} + o(\delta), \quad (2)$$

where the derivatives are evaluated at (x, t) . By equations (1) and (2) we have

$$W(x, t; \gamma) = V(x, t) - \delta V(x, t)[M_p(\gamma) + M_y(\gamma)] + \delta r M_y(\gamma) + \gamma\delta \frac{\partial V}{\partial x} + \delta \frac{\partial V}{\partial t} + o(\delta). \quad (3)$$

Under the optimal strategy, the choice of instantaneous growth rate at time t maximizes reproductive value. The reproductive value $V(x, t)$ to the parent under the optimal strategy is thus the limit as δ tends to 0 of the maximum value of $W(x, t; \gamma)$:

$$V(x, t) = \lim_{\delta \rightarrow 0} \max_{\gamma} W(x, t; \gamma). \quad (4)$$

Thus, by equations (3) and (4) we have

$$0 = \frac{\partial V}{\partial t} + \max_{\gamma} \left[\gamma \frac{\partial V}{\partial x} - M_p(\gamma)V(x, t) - M_y(\gamma)[V(x, t) - r] \right]. \quad (5)$$

This is the Hamilton-Jacobi-Bellman equation.

We assume that it is never optimal for the parent to desert when the young are still alive, so that $V(x, y) > r$. The optimal strategy of the parent is the value γ^* of γ which maximizes

$$\gamma \frac{\partial V}{\partial x} - M_p(\gamma)V(x, t) - M_y(\gamma)[V(x, t) - r]. \quad (6)$$

Expression (5) can be rearranged to give

$$\frac{\partial V}{\partial t} = \min_{\gamma} \left[M_p(\gamma)V(x, t) + M_y(\gamma)[V(x, t) - r] - \gamma \frac{\partial V}{\partial x} \right]. \quad (7)$$

Expression (7) represents the rate of change of reproductive value with time at the optimal strategy γ^* . The optimal strategy of the parent is the value γ^* of γ which maximizes the expression within the brackets on the right-hand side of expression (5), or equivalently minimizes the expression on the right-hand side of expression (7). The first term within the maximization in expression (5) represents the rate of change of reproductive value due to the parent's foraging option. The second term represents the rate of change of the parent's reproductive value due to parental mortality because if the parent dies, the parent loses the reproductive value V . The third term represents the rate of change of reproductive value to the parent if the young dies because $V - r$ is the loss of reproductive value to the parent if the young dies. The maximization in expression (5) is carried out independently for each x and gives the optimal $\gamma^*(x)$ to be used at each x .

Special case

When R is independent of time, then V is independent of time. The term $\partial V / \partial t$ on the left-hand side of equation (7) equals 0 and

$$0 = \min_{\gamma} \left[M_p(\gamma)V(x) + M_y(\gamma)[V(x) - r] - \gamma \frac{\partial V}{\partial x} \right]. \quad (8)$$

We have shown that γ^* minimizes

$$M_p(\gamma)V(x) + M_y(\gamma)[V(x) - r] - \gamma \frac{\partial V}{\partial x}. \quad (9)$$

In section 1 of the [Appendix](#), we show that this implies that at $\gamma^*(x)$,

$$\frac{\partial V}{\partial x} = \min_{\gamma} \left[\frac{M_p(\gamma)}{\gamma} V(x) + \frac{M_y(\gamma)}{\gamma} [V(x) - r] \right]. \quad (10)$$

We can also derive expression (10) using increments of size rather than increments of time (see [Appendix](#), section 2). Expression (10) represents the rate of change of reproductive value with size at the optimal $\gamma^*(x)$ of γ . When V does not depend on time, the optimal strategy $\gamma^*(x)$ is determined by maximizing expression (9), which is the same as minimizing

$$G(\gamma) = \frac{M_p(\gamma)}{\gamma} V(x) + \frac{M_y(\gamma)}{\gamma} [V(x) - r]. \quad (11)$$

Expression (11) shows that a parent faces a trade-off between minimizing the mortality risk to itself and its young and maximizing the rate at which to provision its young for growth. Expression (11) is a generalized version of the criterion proposed by Gilliam (1982). If mortality to the parent is 0, then expression (11) is the trade-off an individual faces between minimizing mortality risk and maximizing its own growth rate.

Figure 1 illustrates that the optimal strategy minimizes expression (11). All possible strategies lie on and above the trade-off curve of expression (11) with optimal strategies lying on the curve. A parent should be indifferent between strategies with the same value of expression (11) and so should be indifferent between strategies which lie on a line when expression (11) is constant. The optimal strategy lies at the point where a line of constant fitness is tangent to the trade-off curve. $V(x)$ is increasing with x (see Fig. 2), thus the slopes of the lines of constant fitness are $V(x)/[V(x) - r]$ decreasing with x (Fig. 3). Although parameter change moves the optimum around the curve, the optimal strategy will always be found in the bottom left boundary of the convex curve due to the negative slope of the lines of constant fitness.

Figure 1 also illustrates the trade-off a parent faces between minimizing the ratio $M_p(\gamma)/\gamma$ and the ratio $M_y(\gamma)/\gamma$ because decreasing one increases the other. As $V(x)$ moves away from r , the optimal strategy tends towards the bottom right of the curve. The solution to the minimization yields a greater mortality rate per unit growth rate for the parent and a lower mortality rate per unit growth rate for the young. As the young grow in size and value, a parent behaving optimally will accept a higher mortality risk for itself to reduce the mortality risk for its young. This is achieved through a reduced growth rate for the young.

Table 1. Parameters and baseline values

Parameter	Definition	Baseline value
x_{max}	Critical size of the young to achieve independence	10,000
R	Reproductive value to the parent when the young reach independence	9
r	Future reproductive success of the parent	1
j_p	Background mortality risk to the parent	0.5
k_p	Mortality risk associated with parental behaviour to the parent	0.3
j_y	Background mortality risk to the young	0.6
k_y	Mortality risk associated with parental behaviour to the young	0.8

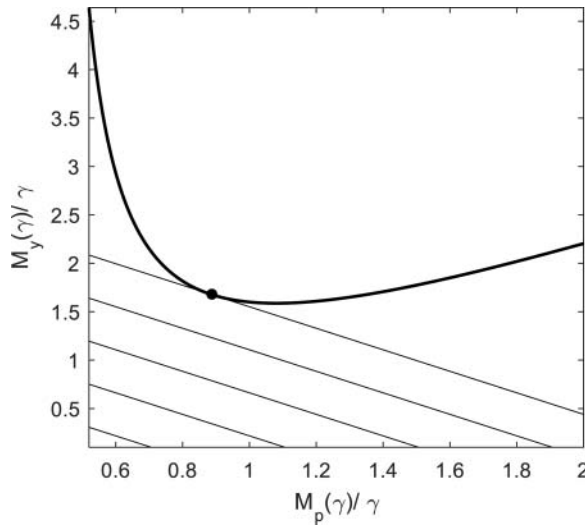


Fig. 1. Curve showing the trade-off between mortality of the young and mortality of the parent. A trade-off exists because increasing one mortality decreases the other. The optimal strategy $\gamma^*(x)$ (solid circle) minimizes $G(\gamma)$ (see expression 11) along the curve. A line of constant G is a straight line in the $(M_p(\gamma)/\gamma, M_y(\gamma)/\gamma)$ plane with slope $V(x)/[V(x) - r]$ for given values of $V(x)$. The optimal strategy lies at the point where a line of constant G is tangent to the curve. Parameter changes will move the optimum around the curve. Unless otherwise stated, parameters have baseline values (see Table 1). $V(x) = 10$.

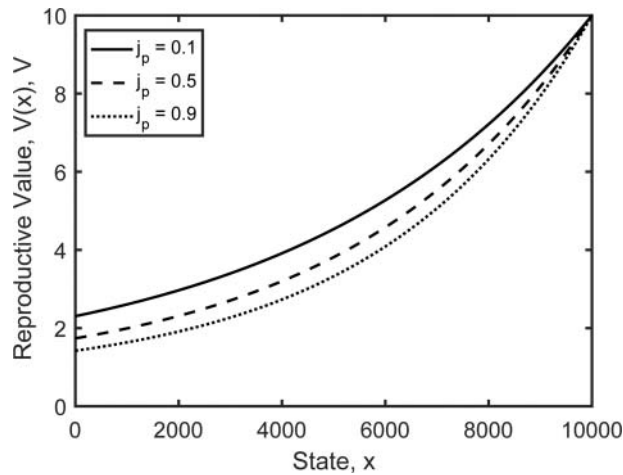


Fig. 2. The reproductive value to the parent $V(x)$ is an increasing, accelerating function of the size of the young, x . With time, $V(x)$ moves away from the residual reproductive value, r . Young must reach the critical size x_{max} to achieve independence. As the young grow in size and become closer to x_{max} , they become more valuable to the parent. When other mortality parameters have baseline values, a change of the parameter j_p is shown. A similar effect is found for changes in other mortality parameters. Unless otherwise stated, parameters have baseline values.

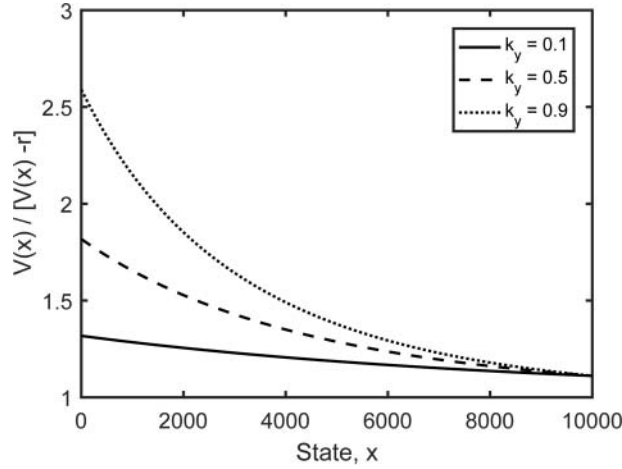


Fig. 3. The slope of the lines of constant fitness $V(x)/[V(x) - r]$ against the size of the young x for a change of the parameter k_y when other mortality parameters have baseline values. A similar effect is found for changes in other mortality parameters.

Worked example

Parent birds and their young are subject to background mortality as well as mortality associated with the parent's behaviour. In our model, we consider both the background mortality as well as mortality attributed to parental behaviour for both the parent and its young. We consider the mortality functions

$$M_p(\gamma) = j_p + k_p \gamma \quad (12)$$

and

$$M_y(\gamma) = j_y + k_y \gamma^2. \quad (13)$$

The parameters j_p and j_y represent constant background mortality to the parent and young respectively because not all mortality is dependent on parental behaviour. The parameters k_p and k_y represent the mortality associated with the growth rate γ for the young to the parent and young respectively. Both mortality functions (12) and (13) are increasing with γ .

The young's mortality function is accelerating, with γ representing the accelerating mortality to the young as the parent increases its growth rate. The young's mortality function would be non-linear if the time the parent is away from the nest disproportionately affects the mortality of the young, whereas it would be linear if the attention of a predator is drawn by the parent visiting the nest. We assume that mortality functions are independent of time, and that the reproductive value of young are independent of time. It follows that reproductive value V is independent of time and thus is only dependent on the size of the young x . We can find the optimal strategy $\gamma^*(x)$ that minimizes expression (11) when the mortality functions are of the form in expressions (12) and (13). Differentiating $G(\gamma)$ in expression (11) with respect to γ gives

$$G'(\gamma) = \left[\frac{M'_p(\gamma)\gamma - M_p(\gamma)}{\gamma^2} \right] V(x) + \left[\frac{M'_y(\gamma)\gamma - M_y(\gamma)}{\gamma^2} \right] [V(x) - r]. \quad (14)$$

If γ^* is the value of γ that minimizes $G'(\gamma)$, then $G'(\gamma^*) = 0$ and solving for γ^* gives

$$\gamma^*(x) = \sqrt{\frac{j_y}{k_y} + \frac{j_p V(x)}{k_y [V(x) - r]}}. \quad (15)$$

RESULTS

Our model assumes that the young become independent when they reach a critical size x_{max} . When the reproductive value to the parent is independent of time, it is just a function of x . In many bird species, pre-fledging mass predicts survival to breeding age (see Schwagmeyer and Mock, 2008) and therefore is an indicator of the value of the young to the parent. The reproductive value to the parent when the young become independent can be written as $V(x_{max}) = R$. The terminal reproductive value R can be derived from an animal's life history. Starting from R and using expression (10), previous values of $V(x)$ can be determined using numerical methods. It is always the case that $V(x)$ is an increasing, accelerating function of x (see [Appendix](#), section 3) and the young become increasingly more valuable to the parent with size (see Fig. 2).

Figure 4 illustrates that the optimal growth rate decreases and decelerates with x when mortality functions are of the forms in expressions (12) and (13). As the young grow in size

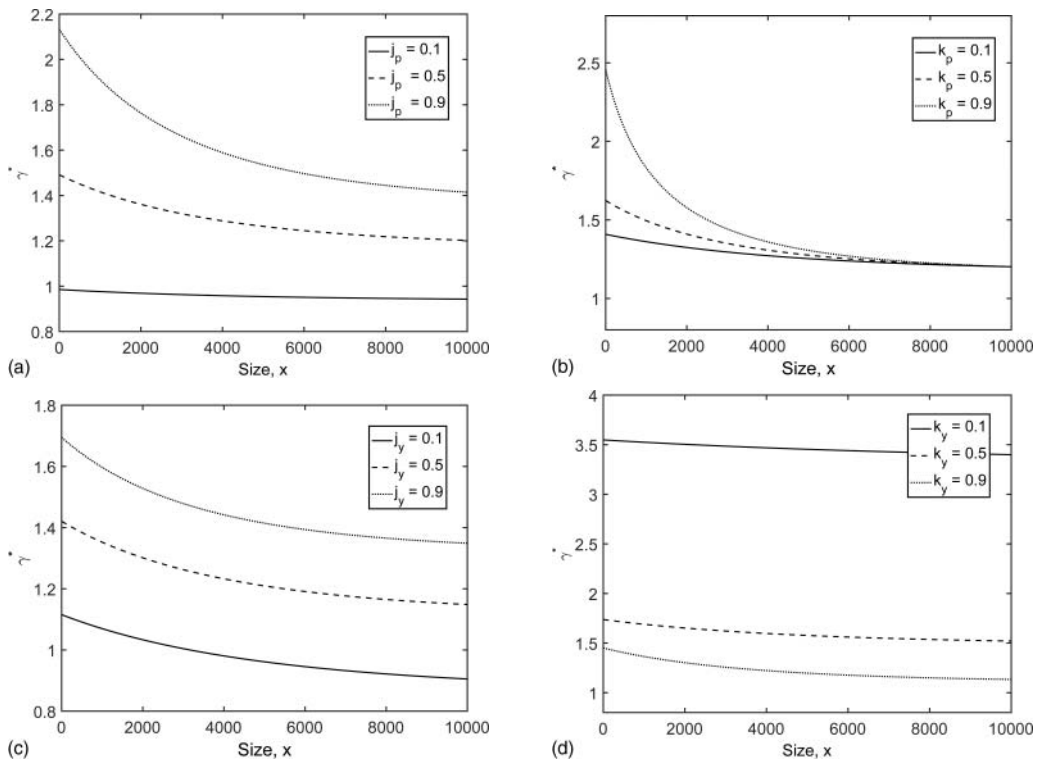


Fig. 4. The optimal growth rate $\gamma^*(x)$ against the size of the young x for varying mortality parameters j_p , k_p , j_y , and k_y . Unless otherwise stated, parameters have baseline values.

and value, a parent behaving optimally should reduce the growth rate for its young. A parent who reduces its provisioning rate can allocate time to other activities, e.g. being vigilant for predators. In this case, a parent behaving optimally should invest a greater proportion of time being vigilant for predators as opposed to foraging for energy for the young as the young grow in size and value.

The forms of the mortality functions in equations (12) and (13), which include background mortality risk and mortality risk associated with parental behaviour for both parent and young, generate novel results. For a given x , an increase of the optimal growth rate is associated with increasing values of the parameters, j_p , k_p , or j_y (Fig. 4a, b, c) when other parameters are held fixed. A parent behaving optimally should spend a greater proportion of time foraging for energy for the young so the young reach independence as soon as possible. An opposite effect is predicted with increasing value of the mortality parameter k_y (cf. McNamara and Houston, 1994); for a given x , and when other parameters are held fixed, the optimal growth rate declines with increasing value of k_y .

Mortality risk that arises from parental behaviour is described in our model by the mortality parameters k_y and k_p . A foraging parent may control these types of risk by foraging in habitats associated with different levels of predation. When mortality risk to the parent $M_p(\gamma)$ and background mortality risk to the young (j_y) are held fixed, the behaviour of the parent cannot change these risks but the parent can control the risk k_y associated with its provisioning behaviour. Skutch (1949) suggests that nest predation increases with activity of parents at the nest. As predators may detect the nest by observing feeding adults, parents should reduce nest visit rates and lower nestling feeding rates to avoid nest predation. This has been found for hole- and cavity-nesting birds (Perrins, 1965; Young, 1996). Figure 4b shows that a parent should change its provisioning rate more for a small change of the parameter k_p when x is small as opposed to when x is large. For small x , a parent behaving optimally should increase its provisioning rate with increasing value of the mortality parameter k_p . For large x , the parent should invest very little foraging effort whatever the change in value of k_p . Figure 5 shows, for a given x , that a change to the mortality parameter k_y prompts the greatest change in the optimal growth rate. These results may suggest that parents change their behaviour more when they can control one type of mortality risk over another.

Not all mortality risk is dependent on parental behaviour. In our model, the parameters j_p and j_y represent constant background mortality to the parent and young respectively. When parental behaviour is characterized by nest visitation frequency to provision young for growth, a parent cannot control the predation risk to itself or its young through its behaviour if behaviour has no effect on predation risk. Since a parent cannot control this type of predation risk, parents are under pressure to reduce the time itself and its young are exposed to this type of mortality. Some snakes and nocturnal mammalian predators use non-visual clues to detect their prey (Woodworth, 1997; Sloan *et al.*, 1998; Degraaf *et al.*, 1999). In this case, reducing the rate of visits to the nest would be an ineffective strategy to reduce predation risk.

DISCUSSION

Using an optimality model, we establish new formulae to describe parental behaviour when there is a trade-off between growth rate of the young and mortality risk to both parent and young. We derive a general expression which accounts for time as well as a case where

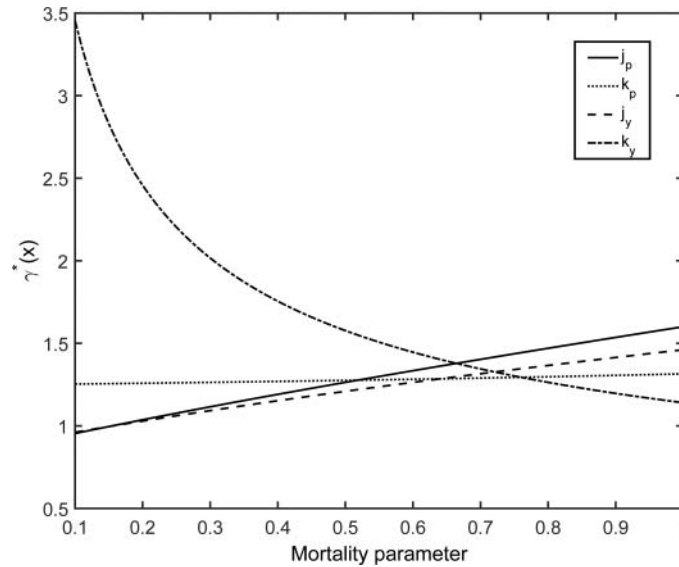


Fig. 5. The optimal growth rate $\gamma^*(x)$ against mortality parameters j_p , k_p , j_y , and k_y for size of the young $x = 5000$.

reproductive value is independent of time and only depends on the size of the young, x . We illustrate our approach with a worked example. Whereas others consider mortality as one parameter (Clark and Ydenberg, 1990; Royle *et al.*, 2014), we describe mortality by four effects: background mortality risk and mortality risk arising from the provisioning rate of the parent for both parent and young. Mortality functions of this form generate novel results. Our model highlights the need to describe mortality by multiple effects to fully predict parental behaviour when there is a trade-off between growth rate and mortality risk.

When reproductive value is dependent on time and size of the young, the optimal strategy of the parent maximizes expression (6), which is a more general version of the condition given by Houston and McNamara (1989).

Gilliam (1982) considered an animal that had to grow to a certain size before it could reproduce and derived the rule, coined the Gilliam criterion, that an animal should minimize mortality risk per unit of growth when it faces a trade-off between foraging for energy and predation risk. A special case of our model considers young that must reach a critical size to achieve independence and reproductive value is independent of time. We show that the optimal strategy $\gamma^*(x)$ of the parent is determined by minimizing expression (11). In our model, a parent faces a trade-off between minimizing the mortality risk to itself and its young and maximizing the rate at which to provision its young for growth. Expression (11) is therefore a generalization of the Gilliam criterion. Furthermore, a parent faces a trade-off between minimizing the ratio $M_p(\gamma)/\gamma$ and the ratio $M_y(\gamma)/\gamma$ because decreasing one increases the other (Fig. 1). Our model predicts that a change in the size and value of the young produces a change in mortality risk to the parent and young through the optimal behaviour of the parent. Studies have found a decline in parental provisioning rate during a breeding attempt (e.g. Naef-Daenzer *et al.*, 2000) and the increasing value of the current young in terms of inclusive fitness has been suggested as an explanation (Winkler, 1987). We

predict that as the young grow in size and value, a parent behaving optimally should reduce its provisioning rate (Fig. 4), thus accepting a greater mortality risk per unit growth to itself to reduce the mortality risk to its young (see Fig. 1). The shape of the curve of reproductive value with increasing size of the young (Fig. 2) is dependent on the assumption that the young must reach a critical size x_{max} to achieve independence. Young that do not reach x_{max} do not survive. In the common tern *Sterna hirundo*, chicks are not able to leave the colony and be fully independent before a critical threshold mass is reached (Schauroth and Becker, 2008). It should be noted that it is not always the case that young must reach a critical size to achieve independence.

In our model, we make the assumption that it is never optimal for the parent to desert when the young are still alive, therefore $V > r$, where r represents residual reproductive value. In our model, we take r as fixed. Instead, we could consider r as dependent on the environment. For instance, if it is either a 'good' or a 'bad' year, r can be the expected breeding success of the next year. If a 'good' year tends to follow a 'bad' year, the value of a parent's current young in a 'bad' year may not be as great as the expected value of the parent's young in the following 'good' year, thus $V < r$. The parent should then abandon the current young and accept r .

Our analysis assumes mortality is dependent on γ but not x . In doing so, we have taken growth rate to be synonymous with the rate of food provisioning. However, we might expect the metabolic rate of the young to increase with their size. Thus for a given rate of food provisioning, growth rate will decrease with size. We have not included this in our model but this could be a possible addition in future work.

In previous models of the trade-off between growth rate and mortality risk in the context of parents feeding young, mortality risk is often described as a single parameter (Clark and Ydenberg, 1990; Scheuerlein and Gwinner, 2006; Ghalambor *et al.*, 2013; Royle *et al.*, 2014). Scheuerlein and Gwinner (2006) suggest that the rate of nest visits is reduced in order to reduce predation risk to the parent rather than the young. Scheuerlein and Gwinner (2006) define predation risk as the observation of predators present in the territory. It is not clear how such predation risk can be determined as predation risk to the parent rather than the young. Our model allows us to consider the predation risk to the young through the inclusion of the mortality function in expression (11) and, unlike previous studies (Ghalambor *et al.*, 2013), also allows us to consider the predation risk to the parent through the inclusion of the mortality function in expression (12). Our model predicts that when all other mortality parameters are held fixed, a parent behaving optimally will increase its provisioning rate with an increase in the parameter that represents background mortality to the parent, j_p (Fig. 4a). An increase in the parental provisioning rate is also predicted for an increase in the parameter that determines the proportion of parental effort that contributes to the mortality of the parent, k_p (Fig. 4b). Ghalambor and Martin (2001) do consider predation risk to parents versus offspring but again describe predation risk to each by a single parameter. Through our illustration, we show that mortality risk should be described by multiple parameters to give a better prediction of parental behaviour. Increasing different aspects of predation risk predicts different resulting optimal behaviours of the parent (cf. McNamara and Houston, 1994). Several empirical studies of parental care in bird species have shown a reduction in parental provisioning rates with an increase in predation risk to the young (Eggers *et al.*, 2008; Martin and Briskie, 2009; Martin, 2011; Zanette *et al.*, 2011; Ghalambor *et al.*, 2013). Our model predicts that when all other mortality parameters are held fixed, a parent behaving optimally will indeed reduce its provisioning rate with an increase in the parameter that determines the proportion of

parental effort that contributes to the mortality of the young, k_y (Fig. 4d). However, a parent behaving optimally should increase its provisioning rate when background mortality risk to the young is increased (Fig. 4c). We show that the effect of mortality risk to the young on the parent's behaviour cannot be fully understood using one parameter alone.

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