

How should breeders react when aided by helpers?

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In cooperatively breeding systems, breeders may reduce their provisioning to the brood when aided by helpers. However, this is found in only some species, and the reasons for the different reactions of breeders are far from clear. Recently, a paradoxical case of breeders in the azure-winged magpie, *Cyanopica cyanus*, increasing their contribution when aided by helpers has further complicated the issue. Existing models on the response of breeders consider only whether helpers contribute to increase the amount of food delivered to the brood. Helpers, however, can also contribute with other types of help that may increase the value of the whole brood for parents, such as reducing predation rate. Here we present a deterministic decision-making model to predict how parents should reduce or increase their parental effort on the basis of the relative role of both types of helpers' contributions: delivering food and/or dispensing protection against predation. The model can be used by field workers to make qualitative and quantitative predictions with their data. As an example, we show how data for the azure-winged magpie predicts the observed increase of parental contribution in the presence of helpers.

Keywords: azure-winged magpie; cooperative breeding; *Cyanopica cyanus*; helpers; optimal investment; parental care; provisioning

In cooperatively breeding species, parents may be assisted by other individuals to rear the brood (Brown 1987; Stacey & Koenig 1990; Koenig & Dickinson 2004). The assistance of helpers may not occur in all reproductive attempts, so, accepting that rearing a brood without the assistance of helpers may demand a higher effort from parents than that when helpers are present, parents should be prepared to react by adjusting their parental investment according to whether they are going to have assistants. Reviews of co-operatively breeding species show that parents can react to the presence of helpers either by compensatorily reducing their parental effort or by maintaining the same level of care (see Hatchwell 1999; Koenig & Dickinson 2004). Their decision may have consequences on the success of the current breeding attempt but also on their chances to perform new attempts within the same season or in future seasons (Clutton-Brock 1991; Heinsohn 2004).

Hatchwell (1999), based on the ideas suggested by Emlen & Wrege (1991) and Hatchwell & Russell (1996), proposed that parents may show compensatory reduction of care in the presence of helpers depending on the nature of the main causes operating on chick mortality. Thus, if the main cause of nest failure is starvation, parents should not reduce care and helpers' contribution will be additive. In contrast, if starvation is rare and other factors such as predation have greater impact on nest success, parents will show a compensatory reduction of care according to helpers' contribution (Hatchwell 1999). Comparative results (Hatchwell 1999) support the association between starvation and additive parental behaviour. However, some cases appear not to fit into this dichotomy, suggesting that other factors may be at work. For instance, in the cooperatively breeding laughing kookaburra, *Dacelo nova-guineae*, the main cause of lost productivity is chick starvation, but helpers failed to increase overall provisioning, and helpers themselves, as well as breeders, compensatorily reduced their feeding contributions as additional helpers were recruited (Legge 2000). A similar situation occurs in white-throated magpie-jays, *Calocitta formosa*

(Innes & Johnston 1996; Langen & Vehrencamp 1999), where the main cause of mortality appears to be starvation but extra provisioning may not have an effect of reducing chick mortality, perhaps due to nestling competition. Recent work with the azure-winged magpie, *Cyanopica cyanus* (Valencia et al. 2006a), has extended the range of variation of possible responses of parents. In this cooperative bird of southern Iberia, chick starvation is scarce and, contrary to expectations, neither breeders nor helpers reduced their provisioning rate with the additional workforce at the nest but even parents clearly increased it when aided by helpers (Valencia et al. 2006a). Until Valencia et al. (2006a), the possibility that breeders react to the presence of helpers by increasing their net contribution was never considered by empirical or theoretical literature on cooperative breeding (reviewed in Koenig & Dickinson 2004; see also the model by Heinsohn 2004). This fact stresses that the way in which breeders respond to the contribution of helpers is poorly elucidated, despite it being a key question in our study of the adaptive nature of helping.

There are different ways in which helpers may contribute to the success of the brood. One way is the addition of provisioning to that delivered by parents to the brood. In this case, the expected benefits for parents are equivalent to the benefits obtained if they had increased their provisioning but without increasing their costs. Another way may increase the expected success of the brood beyond the possibilities of the parents alone, for example if helpers contribute to reduce predation risks by increasing the workforce to detect or to repel predators or to successfully defend the family territory against rivals. In this case, the expected benefits for parents may be higher than the maximum benefits they would obtain alone even by allocating extremely high amounts of expenditure, a possibility that has not been considered in previous models (Hatchwell 1999; Cant & Field 2001; Heinsohn 2004). These two types of helping may roughly correspond to what have been called unshared and shared parental care (see e.g. Clutton-Brock 1991), but their relevant feature for the purpose of a parental care model is the way in which they can affect the curve of parent benefits (see below). Both forms of helping may occur simultaneously and their relative contributions to brood success may be variable. Here we present a deterministic, general decision-making model to predict the reaction of parents to the presence of helpers as a function of the relative importance of these two types of helpers' contributions.

THE MODEL

Preliminary Simplifications

Our model is intended to present a basic framework to predict the reaction of parents when assisted by helpers. Parents' reactions may be modulated by the effect of the assistance on the helpers themselves, for instance when helpers and breeders are relatives. However, here we will not consider these possible effects on helpers and will include only the point of view of parents when they receive some contribution from others, which potentially increases the expected success of brood rearing.

Here we use cost and benefit functions, which have the advantages that their parameters can be estimated from fieldwork, to make quantitative predictions on parents' reaction. However, we also provide a more general argument on the behaviour of breeders when assisted by helpers in Appendix 1.

Parents' reactions may depend on the types of functions used for costs and benefits. The use of a general benefit function has the advantage of generality but does not allow analytical solutions that could be used to test single case examples. We will use both a concrete benefit function (Bertalanffy type) in the main text and a more general function in Appendix 2. Finally, we will compare the results when using both the concrete and the more general benefit functions.

Benefit and Cost Functions for Parental Expenditure

Assume that an individual parent (either sex) obtains benefits, B , according to a Bertalanffy-type function of the amount of parental expenditure, x , devoted to current offspring as follows:

$$B = k(1 - e^{-a(x - x_{\min})}) \quad \text{when } x \geq x_{\min};$$

$$B = 0; \quad \text{when } 0 \leq x < x_{\min};$$

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Parameter k is the asymptote value of the benefit curve, which represents the maximum benefits that the parent is expected to obtain when providing infinite parental care to current offspring. Parameter a (with opposite units to parental expenditure) affects the steepness at which the benefit curve approaches the asymptotic value k as expenditure x increases (i.e. the larger is a the larger is the steepness of the slope towards the asymptotic value k ; see Fig. 1). Parameter x_{\min} is a constant that assumes the minimum offspring expenditure to obtain positive benefits.

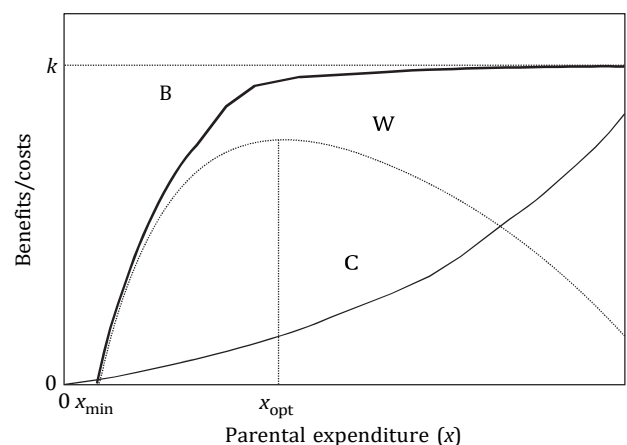


Figure 1. Benefit-cost curves (B and C , respectively) in relation to parental expenditure. W (broken line) represents the difference between benefits and costs for each parental expenditure and x_{opt} the amount of expenditure for which the difference between benefit and cost is maximum. x_{min} represents the minimum expenditure to obtain positive benefit (see model description).

Assume that reproductive costs, C , increase exponentially as a function of the parental expenditure x as follows:

$$C \propto x^b \left(e^{bx} - 1 \right); \quad \delta 2b$$

where c is a proportionality constant and b is a parameter affecting the rate of increment of costs when x increases (the larger is b the larger is the rate of increment of costs with x ; see Fig. 1). Both benefit and cost curves begin from zero when there is no parental expenditure. The profitability of the decision on the amount of parental expenditure, W , can be obtained from the difference between benefit and cost functions in equations (1) and (2):

$$W \propto x^b \left[k \left(1 - e^{-a\delta x - x_{\min}^b} \right) - c \left(e^{bx} - 1 \right) \right]; \quad \text{when } x \geq x_{\min};$$

$$W \propto x^b \left[-c \left(e^{bx} - 1 \right) \right]; \quad \text{when } 0 \leq x < x_{\min}; \quad \delta 3b$$

Optimal expenditure, x_{opt} (see Fig. 1), is defined by the value that maximizes function in equation (3). We assumed that $x_{\text{opt}} \geq x_{\min}$; then

$$\frac{dW}{dx} \Big|_{x=x_{\text{opt}}} \propto k a e^{-a\delta x_{\text{opt}} - x_{\min}^b} - c b e^{b x_{\text{opt}}} \propto 0; \quad \delta 4b$$

from which

$$x_{\text{opt}} \propto \frac{1}{a b} \ln \frac{k a}{c b}; \quad \delta 5b$$

where $\ln(x)$ represents the natural logarithm of x . Therefore, optimal parental expenditure, x_{opt} , increases when b decreases (Fig. 1). Equation (5) imposes some restriction to the possible values of b because x_{opt} must be higher than x_{\min} . For example, for $x_{\min} \propto 0$ and $k \propto c$, the range of possible values of b is $0 < b \leq a$.

Effect of Helping on Optimal Parental Expenditure

We consider two types of helping. Type I help is the addition of provisioning to that delivered by parents to the brood. In this case the expected benefits for parents are equivalent to the benefits obtained if they had increased their own provisioning but without increasing costs. Type II help increases the expected success of the brood beyond the possibilities of parents alone (e.g. by reducing predation risks or increasing the chances of successful territory defence). Under this type II help, the expected benefits for parents can be higher than the maximum benefits they would be able to obtain alone, even by allocating extremely high amounts of expenditure, thus increasing the asymptote value of the benefit function. We included these contributions in the model by adding two positive parameters, p and t , to the benefit function, B_1 (see Fig. 2),

$$B_1 \propto x^b \left[k t \left(1 - e^{-a\delta x - x_{\min}^b p} \right) \right]; \quad \text{when } x \geq u \quad \text{and}$$

$$B_1 \propto x^b \propto 0; \quad \text{when } 0 \leq x < u; \quad \delta 6b$$

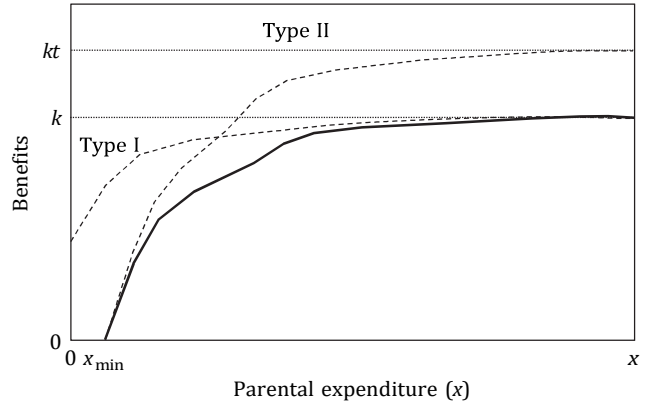


Figure 2. Benefit curves in relation to parental expenditure when the contribution of helpers is considered: (a) for parental contribution alone (continuous line); (b) when helpers provision the brood (type I help; dashed line); (c) when helpers contribute to reduce predation or any other type II help (dotted line). Asymptotic benefits are indicated from parental care and type I help alone (k) or when type II help is added (kt).

where u is the maximum of $x_{\min} - p$ and zero. Parameter p ($p \geq 0$) is the expenditure (type I help) that helpers provide, which is simply added to the parental expenditure x . Parameter t ($t > 0$) produces a deviation in the probability of success for the brood due to the presence of helpers (type II help) and therefore proportionally modifies the curve of benefits. The presence of helpers in itself may cause the location of the nest to be more easily detectable, thus favouring predation. In that case, $0 < t < 1$ when helpers only provide food to the chicks. When helpers increase nest protection the net effect is positive (i.e. $t \geq 1$) and helpers' contribution should increase the curve of benefits. Both parameters are assumed to affect the benefits but not the costs for parents because costs for parents depend only on their expenditure x (remember that we are not considering the relatedness between breeders and helpers in this study). The main difference between the effects of both parameters related to helping is that provisioning p (if sufficiently large) produces net benefit at zero parental investment and higher increases of benefits when parental expenditure is relatively low, whereas parameter t increments more the benefit curve for higher values of parental expenditure (Fig. 2).

Thus, the new function for net benefits when parents are aided by helpers is $W_1 \propto B_1 - C$,

$$W_1 \propto x^b \left[k t \left(1 - e^{-a\delta x - x_{\min}^b p} \right) - c \left(e^{bx} - 1 \right) \right]; \quad \text{when } x \geq u \quad \text{and}$$

$$W_1 \propto x^b \left[-c \left(e^{bx} - 1 \right) \right]; \quad \text{when } 0 \leq x < u \quad \delta 7b$$

and the new optimal expenditure for parents when helpers are present, $x_{\text{opt}1}$, is obtained from the value of x that maximizes the new function of benefits W_1 . We assumed that $x_{\text{opt}1} \geq x_{\min}$; then

$$\frac{dW_1}{dx} \Big|_{x=x_{\text{opt}1}} \propto k t a e^{-a\delta x_{\text{opt}1} - x_{\min}^b p} - c b e^{b x_{\text{opt}1}} \propto 0; \quad \delta 8b$$

thus yielding

$$\frac{x_{opt1} - x_{opt}}{x_{opt}} \approx \frac{p \ln \delta t - ap}{a p b} \quad \delta 9p$$

Equation (9) shows the change in optimal expenditure of breeders, $x_{opt1} - x_{opt}$, when assisted by helpers. When helpers contribute only by increasing the net provisioning delivered to the brood (type I), then $t \approx 1$ and, as obtained in previous models (e.g. Heinsohn 2004), parents should compensate their expenditure by reducing their contribution in the value $ap/(a p b)$. A new perspective, not predicted in previous models, arises when helpers' assistance consists of net protection or defence of the territory or the whole brood (type II); then our model predicts that parents should increase their expenditure in the value $\ln(t)/(a p b)$. In the more general case that helpers may provide contributions of both types (type I and type II), parents are expected to increase their expenditure when

$$\ln \delta t > ap \quad \delta 10p$$

and they are expected to compensatorily reduce it when $\ln(t) < ap$. Thus, if t is sufficiently large compared to p , parents should increase their investment and otherwise they should decrease it. The absolute change in optimal expenditure, $x_{opt1} - x_{opt}$, after the assistance provided by the helpers, $q \approx \ln(t) - ap$, follows a parabolic relationship with the rate of increase of the cost function, b (see Fig. 3)

$$Dx_{opt} \approx \frac{q-a}{1 p b} \quad \delta 11p$$

The change in optimal expenditure of breeders when assisted by helpers with respect to the optimal expenditure of breeders alone is

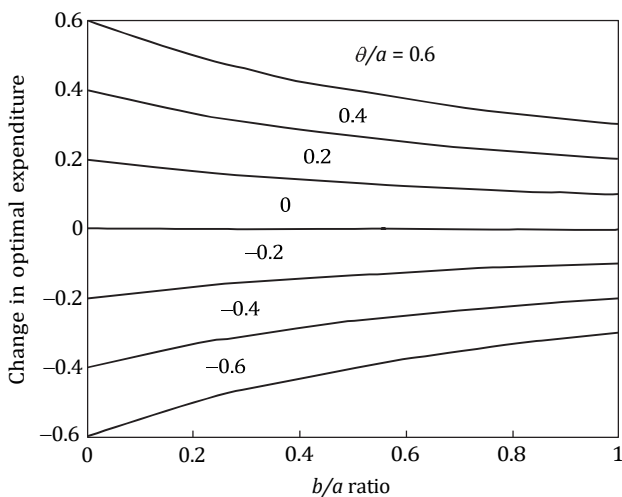


Figure 3. Absolute change in optimal expenditure when helpers are present, Dx_{opt} , in relation to the type of help, q/a , and the ratio of the steepness parameters of the cost function relative to the benefit function, b/a .

$$\frac{x_{opt1} - x_{opt}}{x_{opt}} \approx \frac{1}{ax_{min}} \frac{p \ln \delta t - ap}{p \ln \delta ka = cb} \quad \delta 12p$$

The relative change in optimal expenditure (in both compensatory and increasing cases) increases with t and b . Therefore, as predicted by the theory, the larger is the rate of increment of cost function with x (i.e. the larger is b) the larger is the change that breeders should show in their expenditure when assisted by helpers. The variation of this variable with parameters a and p is a little bit more complicated because it is also dependent on the values of other parameters.

Quantitative predictions of optimal parental expenditure (equations (9) and (11)) are not highly dependent on the type of benefit function used. Appendix 2 summarizes the reactions of breeders in relation to the care that helpers provide when we use a more general sigmoidal-type benefit function (equation (Ab)). Curves in Fig. A1 represent the transition lines between regions where parents should increase (left side of the lines) or compensate (right side of the lines) their expenditure after the helpers' contribution. Exponential function, $t \approx e^{ap}$, in this figure represents the case of a single Bertalanffy-type benefit function; other curves represent the more general sigmoidal-type benefit functions. The use of a general sigmoidal-type benefit function does not allow analytical solutions that could be used to test single case examples. Thus, we will use the single-benefit Bertalanffy-type function to compare qualitative and quantitative predictions of the model with real data (next section).

Real Data Example: Parents' Reaction in the Azure-winged Magpie

To obtain a quantitative prediction from our model with real data, we estimated the values of parameters t and p for a cooperative breeding bird, the azure-winged magpie, from the study by Valencia et al. (2006a). In that study, the presence of helpers related to reduced predation rates for the brood. Of 56 nests for which at least one chick hatched, 20 of 30 nests survived until fledgling with the presence of helpers whereas only eight of 26 nests survived without helpers. Therefore, parameter t for the effect of helpers on the chances for a brood to survive predation was $t \approx 2.17$ (i.e. the ratio of survival chances for the brood with and without helpers).

Helpers in the azure-winged magpie also contributed to provisioning the nest. Total provisioning rate was 0.68 visits/h higher in nests with helpers than in nests without helpers (see Fig. 5 in Valencia et al. 2006a). This increment in the provisioning rate included the reaction of helped parents who contributed on average 0.18 visits/h more than unhelped parents (see Fig. 1 in Valencia et al. 2006a) and the mean contribution of helpers to provisioning the brood, which is parameter $p \approx 0.50$ visits/h.

Unpublished data on the relationship between parental expenditure (i.e. provisioning rate) and number of fledglings from fieldwork by J. Valencia and C. de la Cruz were used to estimate parameter a . We used the nonlinear

estimation procedure implemented in Statistica 6.0 (Stat-Soft 2001) to fit field observations from 108 nests on the number of fledglings in relation to the provisioning rates of breeders to a Bertalanffy-type (i.e. $y \approx f(1 - e^{-ax})$) curve. Regression fit was carried out using the simplex and quasi-Newton method to calculate regression coefficients. This procedure provided the values $f \approx 4.49 \pm 0.14$ (mean \pm SE; $P < 0.001$) fledglings and $a \approx 0.83 \pm 0.29$ (visits/h) $^{-1}$ ($P < 0.01$).

Working with the above parameters, a , p and t , we found that the product $ap \approx 0.41$ is lower than $\ln(t) \approx 0.77$, which represents the region of the phase diagram where parents should increase their expenditure when helpers are present (see exponential curve, $t \approx e^{ap}$, in Fig. A1). We lack precise information on the value of parameter b for the cost function. However, assuming that a realistic value of $b \approx 0.8$ (i.e. the steepness at which the cost curve increment is near equal to the steepness at which the benefit function approaches the asymptotic value), equation (9) predicts an increase in their expenditure in the value 0.23 visits/h, notably close to the observed increase of 0.18 visits/h (Valencia et al. 2006a).

DISCUSSION

We have presented a model that incorporates two types of helpers' contributions that potentially affect the curve of benefits for breeders in different manners. Parents' decisions on optimal amount of care should be sensitive to the curve of benefits, which must include not only the effects of food provisioning but also the chances of survival and future success of offspring caused by any other factors, provided that they are feasibly assessed by parents. This idea is rarely incorporated in the literature on cooperative breeding (Koenig & Dickinson 2004; but see Valencia et al. 2006a), although it is quite common in studies on parental investment. For instance, parents may stop their investment when the chances of success fall due to external causes (e.g. high probability of predation, infanticide or unfavourable weather conditions: Bruce 1960; Haig 1990; Hakkarainen & Korpimäki 1994) or they may increase it when the expectations for future success of offspring increase due for example to higher quality of mates (De Lope & Moller 1993), eggs (Moreno & Osorno 2003; Moreno et al. 2004) or nests (Soler et al. 2001; De Neve & Soler 2002). By incorporating these types of effects, our model can explain the paradoxical increase of parental investment when helpers add their provisioning, provided that their presence also increases the success of the brood beyond provisioning itself, for instance by reducing predation (see Hatchwell 1999; Legge 2000; Koenig & Dickinson 2004) or by increasing offspring quality (Hatchwell et al. 2004; Russell 2004; Valencia et al. 2006b).

The intuitive idea that parents should not compensate when starvation is an important cause of chick mortality (Emlen & Wrege 1991; Hatchwell & Russell 1996; Hatchwell 1999) is fully compatible with our model. Hatchwell (1999) presented this idea using a graphical model with cost and benefit curves, arguing that when parental care is within the region when the slope of the

benefit curve is lower than that of costs (right side of the graph in his Fig. 3) parents should reduce their effort in the presence of helpers and not otherwise (left side of the graph). Our model follows a different rationale and assumes that parents will tend to invest an optimal amount of care according to their benefit and cost curves. Hence, they should reduce their care if it were in the right-side region of Hatchwell's model even without any contribution of helpers because in this right-side region the benefits increase slowly but the costs increase quickly. The agreement about a possible relationship with starvation emerges when we consider optimum care for benefit/cost curves of different parameters a and b and the contributions of the helpers. In our model, the optimum expenditure (equation (5)) is closer to the right-hand side position when parameter a is high and/or parameter b is low. Thus, compensatory reduction of care by parents (i.e. when $t \approx 0$; see equations (9) and (12)) is more likely when the benefit curve approaches quickly to the asymptote and the cost curve increases slowly so that optimal care occurs near the asymptote of the benefit curve and hence starvation should be less common. Therefore, our model is likely to conform with many of the qualitative results presented in the reviews of Hatchwell (1999) and Legge (2000), although published information is usually insufficient to allow quantitative predictions. For example, if main helpers' effect on brood success is due to reducing predation rather than to increasing food provisioning, our model would tend to predict no reduction or even incremental increases of care by parents. However, five of 16 species in Hatchwell's review (Table 1 of Hatchwell 1999) show reduced predation coupled with parents' compensation. For all these cases we would need at least data on the benefit curve and on the quantitative contribution of helpers on provisioning and reducing predation to test whether they conform with our model's predictions.

The model presented here is easily applicable to real data as we have shown with the example for the azure-winged magpie. It is the curve of costs that is certainly most difficult to determine from field data. However, as helpers have no effect on the cost function, we might obtain quantitative predictions after making some assumptions on the steepness of the cost curve (parameter b).

It would be particularly interesting to use the model to explain those cases that depart from qualitative expectations in published reviews. For example, the main exceptions in Hatchwell (1999) comparative work are the laughing kookaburra, and the white-throated magpie-jays. In both species parents reduce their effort when helpers contribute to feed the young despite starvation and partial brood losses being common (Innes & Johnston 1996; Langen & Vehrencamp 1999; Legge 2000). A common feature in these two species is that sibling competition is common, even leading to siblicide (Innes & Johnston 1996; Langen & Vehrencamp 1999; Legge 2000). Interactions within the brood may prevent further parental care from providing benefits above a certain level of brood success. We would suggest, pending empirical testing, that sibling competition might limit the asymptote of brood success to a forced low value, so that

starvation may still be likely but further benefits unlikely, driving parents (and helpers) to be more willing to reduce their effort when other individuals join the group.

It is noteworthy that in our analysis the steepness of the cost curve has no effect on the qualitative prediction about parents' reactions (i.e. in the decision about increase or compensate); its effect appears only on the quantitative amount of change. When the cost curve is steeper (higher b) the change of parents' expenditure is smaller in absolute terms (see equation (9)), although it is bigger relative to the initial expenditure of parents in the absence of helpers because b affects x_{opt} more than the absolute change of parents' expenditure (see equation (12)). This is an important point when considering cost reductions (e.g. load-lightening; Brown 1987) as a reason for parents to compensate (Hatchwell 1999; Legge 2000; Heinsohn 2004). For instance, in kookaburras, it has been argued (Legge 2000) that the unexpected compensatory reaction might be caused by the importance of reducing workload. Reduction of care may certainly have an effect on parents' future success (Heinsohn 2004), but this must have already been taken into account by parents in their decision making on the optimal amount of care in the absence of helpers. Parents should be more willing to reduce their care in the presence of helpers when their optimal expenditure in the absence of helpers is near the asymptote of the benefit curve, which is more likely when costs of care are low rather than high.

Our model considered breeders regardless of their sex. However, note that the benefit/cost curves are at the level of the individual, so variations between sexes should translate into different predictions for their reactions to helping, as data from different species indicate (Hatchwell 1999; Legge 2000). The same applies to variations between years or populations (e.g. Luck 2002). For instance, bad weather conditions may increase the costs of provisioning. Our model predicts that, in bad years, other things being equal, parents will tend to show smaller changes in their parental expenditure in the presence of helpers compared to good years.

Our analysis remains incomplete in several aspects. For instance, relatedness between breeders and helpers may potentially affect the reaction of parents (see e.g. Heinsohn 2004). Another source of departure from the predictions of the model arises when responses by parents may be based on behaviours other than provisioning. The literature on parents' reactions focuses on food provisioning (Hatchwell 1999; Legge 2000; Heinsohn 2004; but see Russell 2004) perhaps because it is an easier way of detecting changes associated with the addition of helpers. However, parents normally provide different types of care. An analysis based only on changes in provisioning rates implicitly assumes that parents' reaction should affect all types of parental contribution equally. This may not be so if, for instance, parents invest more in defence against predation when helpers provide food (see e.g. Russell 2004). It is difficult to evaluate these potential factors without detailed fieldwork on all these behaviours at the same time. Our model may be a first step that deserves future work towards a more comprehensive framework that could incorporate not only different types of behaviours in helpers but also in the responses of helped breeders.

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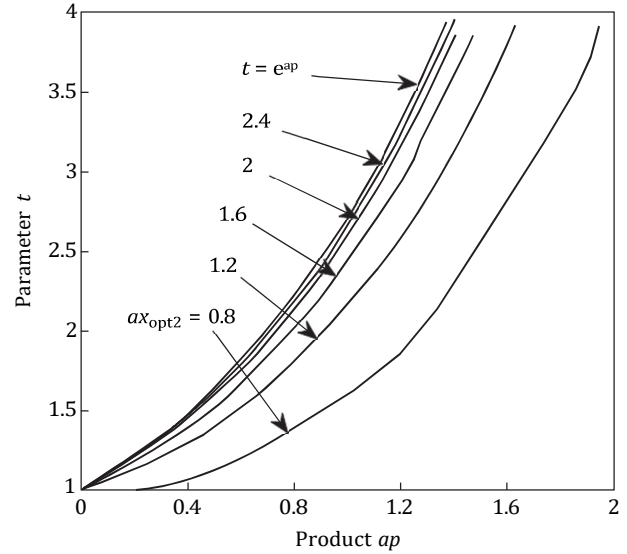


Figure A1. Phase diagram comparing the model when exponential-type ($t = e^{ap}$) or sigmoidal-type functions are used (see model for details). Curves represent transition lines between regions where parents should increase their expenditure (left side of each line) or compensate it (right side of each line). Five curves of the sigmoidal functions are presented at different values of optimal expenditure.

Appendix 1: General Model

The reproductive value (RV) of an individual of age e can be measured as the expected number of chicks in future reproductions

$$RV_e = \sum_{i=e+1}^{\infty} p_i m_i \quad \delta A1b$$

where p_i and m_i are the probability of survival as a breeder and the expected number of chicks, respectively, at year i . The reproductive expenditure of parents in the present generation e decreases their reproductive value, RV_p , due to a decrease in the probability of survival and/or in the future number of chicks. Thus, RV_p should be an accelerated decreasing function with parental expenditure x . Hence,

$$\frac{dRV_p}{dx} < 0 \quad \text{and} \quad \frac{d^2RV_p}{dx^2} < 0; \quad \delta A2b$$

The reproductive value of the brood in the present generation e , RV_b , increases with parental expenditure x . However, the increases in RV_b with x could be a decelerated increasing function, thus satisfying

$$\frac{dRV_b}{dx} > 0 \quad \text{and} \quad \frac{d^2RV_b}{dx^2} < 0; \quad \delta A3b$$

Parents benefit with increases in either their reproductive value or the reproductive value of their broods. Thus, the function being maximized is the sum of these two functions:

$$RV_p + RV_b; \quad \delta A4b$$

However, these functions are oppositely related to the present parental expenditure x . Optimal expenditure, x_{opt} , is defined by the value of x that satisfies

$$-\frac{dRV_p}{dx} = \frac{dRV_b}{dx}; \quad \delta A5b$$

that is, when the marginal reproductive values (derivatives of the RV functions) of parents and brood are equal in magnitude and of opposite sign. This means that the decrease in RV_p due to the parental reproductive effort is compensated by the increase in the RV_b of the brood.

When helpers are present, we assume that their contribution modifies RV_b function but not RV_p function. Therefore, the new optimal expenditure of the breeders, after the helpers' contribution, must satisfy equation (A5) after the change in the marginal reproductive value of the brood: parents should increase their reproductive effort if helpers increase the marginal reproductive value of the brood; otherwise they should decrease it.

In the specific model presented in this study we represent benefits, B , and costs, C , functions instead of RV_b and RV_p functions ($B = RV_b$ and $C = -RV_p$).

Appendix 2: General Benefit Function

Results for optimal parental expenditure (equation (9)) should depend on the benefit function assumed. Here we use a more general function for parent benefits and compare its numerical results with those obtained with the simpler Bertalanffy-type function (equation (1)).

Assume that an individual parent obtains benefits, A , according to a sigmoidal-type function of the amount of parental expenditure x devoted to current brood as

$$A_2(x) = kt \left[1 - \frac{1}{\cosh\left(\frac{a}{2}(x - x_{\min}) - bp\right)} \right]; \text{ when } x \geq u \text{ and}$$

$$A_2(x) = 0; \text{ when } 0 \leq x < u; \quad \delta A6b$$

where u is the maximum value between $x_{\min} - p$ and zero and k represents the maximum benefits that the parent is expected to obtain when providing infinite parental expenditure to the current brood. Parameter a affects the steepness at which the benefit curve approaches the asymptotic value k as expenditure x increases. Parameter x_{\min} is a constant that assumes a minimum parental expenditure to obtain positive benefits, and parameters t and p represent helper contributions (type I and type II, respectively). In this case the derivative of the function (A6) at $x = x_{\min}$ is zero. Thus, a simpler function A_1 may be used by making $x_{\min} = 0$:

$$A_1(x) = kt \left[1 - \frac{1}{\cosh\left(\frac{a}{2}x - bp\right)} \right]; \text{ when } x \geq 0 \text{ and}$$

$$A_1(x) = 0; \text{ when } x < 0; \quad \delta A7b$$

The profitability of the decision on the amount of parental expenditure, W_2 , can be obtained from the difference between benefit and cost functions in equations (A7) and (2):

$$W_2(x) = kt \left[1 - \frac{1}{\cosh\left(\frac{a}{2}x - bp\right)} \right] - c(e^{bx} - 1); \quad \delta A8b$$

The new optimal expenditure for parents when helpers are present, $x_{\text{opt}2}$, is obtained from the value of x that maximizes the new function of benefits W_2 :

$$\frac{dW_2}{dx} = kt \left[\frac{\sinh\left(\frac{a}{2}(x_{\text{opt}2} - bp)\right)}{\cosh^2\left(\frac{a}{2}(x_{\text{opt}2} - bp)\right)} \right] - cbe^{bx_{\text{opt}2}} = 0; \quad \delta A9b$$

Numeric results from equation (A9) show that optimum value of parental expenditure increases when t increases and that $x_{\text{opt}2}$ decreases when p increases, as when using the Bertalanffy-type benefit function (equation (9)). Optimum value for parental expenditure should not change after helper contribution when

$$t \frac{\sinh\left(\frac{a}{2}(x_{\text{opt}2} - bp)\right)}{\sinh(ax_{\text{opt}2})} = \frac{\cosh^2\left(\frac{a}{2}(x_{\text{opt}2} - bp)\right)}{\cosh^2(ax_{\text{opt}2})}; \quad \delta A10b$$

which produces transition lines in the phase diagram similar to the exponential solution, $t = e^{ap}$, obtained when a Bertalanffy-type benefit function is used (see Fig. A1).