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How should breeders react when aided by helpers?

JUAN CARRANZA*, VICENTE POLO†, JULIANA VALENCIA*, CONCHA MATEOS* & CARLOS DE LA CRUZ*
*Biology & Ethology Research Group, University of Extremadura, Spain
†Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales, CSIC, Spain

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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 cooperatively 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 novaguineae*, 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*

Correspondence and present address: J. Carranza, Unidad de Biología y Etología, Facultad de Veterinaria, Universidad de Extremadura, 10071 Cáceres, Spain (email: carranza@unex.es). V. Polo is at Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales, CSIC, José Gutiérrez Abascal 2, 28006 Madrid, Spain. C. de la Cruz is at Area de Zoología, Facultad de Ciencias, Universidad de Extremadura, 06071 Badajoz, Spain.

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(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:

$$B(x) = k\left[1 - \mathrm{e}^{-a(x - x_{\min})}\right], \quad \text{when } x \geq x_{\min}.$$

$$B(x) = 0, \quad \text{when } 0 \leq x < x_{\min}. \tag{1}$$

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.

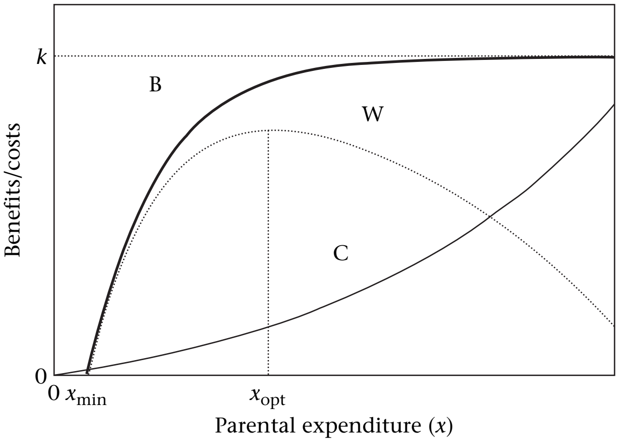

Figure 1. Benefit–cost curves (B and C, respectively) in relation to parental expenditure. W (broken line) represents the difference between benefits and costs for each parental expenditure and x_{opt} the amount of expenditure for which the difference between benefit and cost is maximum. $x_{\min}$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