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Estimating mechanisms and equilibria for offspring begging and parental provisioning

Mathias Kölliker

Department of Biology, Indiana University, Bloomington, IN 47405-3700, USA (mathias.koelliker@swissonline.ch)

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Evolutionary models for the resolution of family conflicts are sensitive to assumptions regarding the behavioural mechanisms regulating parental resource provisioning and offspring begging. Thus, quantitative empirical estimates of the mechanisms are critical to validate current evolutionary models, but a standardized method is lacking. I present a formalization of Hussell's (1988 *Am. Nat.* 131, 175–202) original graphical model of mechanisms regulating the effect of begging on provisioning, and of provisioning on begging, based on linear regression equations. The model makes it possible to estimate quantitatively the behavioural mechanisms and the resulting proximate equilibria for begging and provisioning by the use of appropriate experiments and standard linear regression analysis.

Keywords: family conflict; behavioural mechanisms; begging; parental care; statistical model

1. INTRODUCTION

The regulation of parental provisioning and offspring begging can essentially be understood through knowledge of two behavioural mechanisms. The first is expressed in parents and determines the effect of offspring demand on parental provisioning. It has been termed the 'EDS mechanism' (effect of demand on supply; Parker *et al.* 2002). The second is expressed in the offspring, describes how parental provisioning affects offspring begging and has been termed the 'ESD mechanism' (effect of supply on demand; Parker *et al.* 2002).

Hussell (1988) showed in a graphical model that any combination of two specific functions describing the two mechanisms yields a short-term equilibrium at which offspring begging and parental provisioning should stabilize. Any alteration of one or both mechanisms should lead to a shift in the equilibrium point (Hussell 1988). The model does not include the effects of parent–offspring conflict on evolved offspring and parental behavioural strategies (Godfray 1995; Mock & Parker 1997). Thus, it is not clear how it relates to an evolutionary theory of offspring begging and parental provisioning (Godfray 1995; Mock & Parker 1997; Parker *et al.* 2002). Hussell (1988) himself seemed to assume that begging has to reflect offspring hunger honestly (Godfray 1991) for his models to hold (see Hussell 1988, p. 177). There is no need for the assumption of honesty, however, because the model describes the equilibrium levels of offspring begging and parental provisioning on a proximate level, that is, *given* specific EDS and ESD mechanisms. It is conceptually detached from evolutionary issues concerning the honesty of begging and the resolution of the parent–offspring conflict.

Recently, Mock & Parker (1997) and Parker *et al.* (2002) clarified the link between proximate models of EDS and ESD mechanisms and evolutionary models of family-conflict resolution. The resolution models contain the EDS and ESD mechanisms as specific (often implicit) assumptions defining the way offspring and parents respond to alterations in each other's behaviours when the system is at an evolutionary equilibrium (see Parker *et al.* (2002) for details). Importantly, current resolution models and their predictions are rather sensitive to alterations in the assumed EDS and ESD mechanisms (Johnstone 1996; Parker *et al.* 2002).

The original supply–demand model of Hussell (1988) is purely graphical and only qualitative predictions can be derived from it. Given the sensitivity of evolutionary models of family-conflict resolution to variation in EDS and ESD mechanisms, quantitative empirical estimation of the mechanisms and equilibrium points becomes critical. A standardized statistical method is lacking, however. To this end, I propose a formalization of the graphical model of Hussell (1988) based on linear regression equations.

2. THE MODEL

Hussell (1988) assumed a positive supply function describing the EDS mechanism, and a negative demand function describing the ESD mechanism (figure 1*a*,*b*). The short-term equilibrium is found where the supply and demand functions intersect (Hussell 1988). He considered variation in the positions of the supply and demand functions and its effect on the equilibrium begging and provisioning levels. The slopes of the functions were assumed to be fixed, although variation in the slopes will equally alter the equilibrium point.

Here, I develop a formal and more general model including both the positions and the slopes of the EDS and ESD mechanisms explicitly, that is, as the intercepts and the slopes of regression lines. For the EDS mechanism (figure 1*a*) total provisioning is partitioned into a baseline begging-independent (intercept; a_{EDS}) and a begging-dependent parental-response component (slope; b_{EDS}). Equally, for the ESD mechanism (figure 1*b*) total offspring begging is partitioned into a baseline provisioning-independent (intercept; a_{ESD}) and a provisioning-dependent component (slope; b_{ESD}).

I assume linear relationships between parental provisioning and offspring begging (see also Harper 1986; Hussell 1988). Linear relationships may often not be strictly true descriptions of EDS and ESD mechanisms, and the model can be extended to account for nonlinear associations by the use of nonlinear regression equations, following the algebraic steps described below. Solutions may, however, often be complex mathematically or solvable only numerically (M. Kölliker, unpublished results for quadratic terms and sigmoid curves). From an empirical point of view, there is often no *a priori* reason to fit nonlinear functions to data and/or experimental data to fit such functions are difficult to obtain owing to the large number of experimental groups required. Thus, for simplicity and empirical tractability I will here restrict the model to linear EDS and ESD mechanisms.

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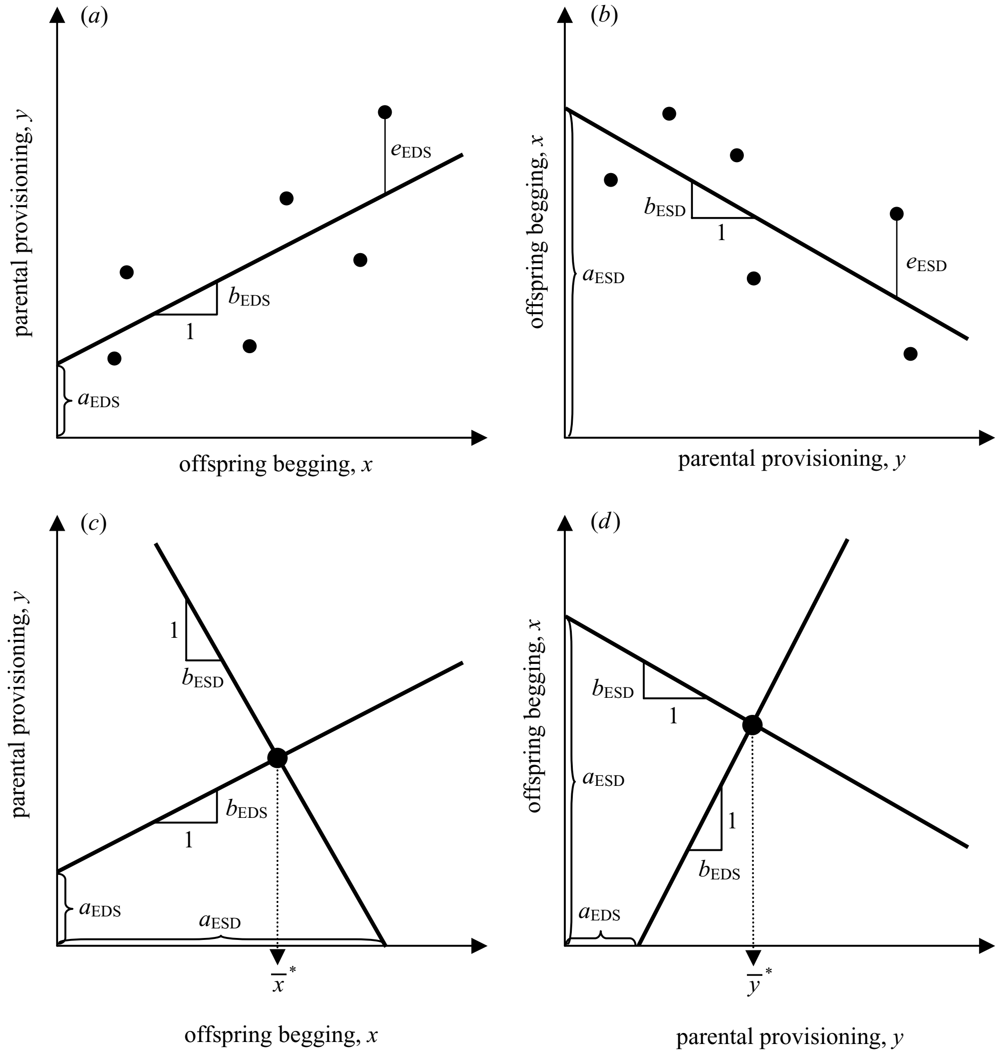

Figure 1. Linear regression lines describing the (*a*) EDS and (*b*) ESD mechanisms. The equilibrium levels (*c*,*d*) are graphically found for begging by superimposing the inverted (*b*) over (*a*). The equilibrium for provisioning is obtained by superimposing the inverted (*a*) over (*b*). See § 2 for formal derivation. The filled circles in (*a*) and (*b*) represent hypothetical individual data points.

Let y be the total parental provisioning to a brood, and x be the total begging level displayed by the brood. The EDS mechanism can be expressed as

$$\hat{y}_{\mathrm{EDS}} = a_{\mathrm{EDS}} + b_{\mathrm{EDS}} x_{\mathrm{EDS}} + e_{\mathrm{EDS}}, \qquad (2.1)$$

where $\hat{y}_{\mathrm{EDS}}$ is the level of provisioning predicted by the EDS mechanism, a_{EDS} is the intercept and b_{EDS} the slope of the least-squares regression line relating parental provisioning to offspring begging (figure 1*a*) and e_{EDS} is the residual variation in parental provisioning (assumed to be normally distributed with mean 0 and variance σ_y^2).

Analogously, the ESD mechanism can be described by

$$\hat{x}_{\mathrm{ESD}} = a_{\mathrm{ESD}} + b_{\mathrm{ESD}} y_{\mathrm{ESD}} + e_{\mathrm{ESD}}, \qquad (2.2)$$

where $\hat{x}_{\mathrm{ESD}}$ is the level of begging predicted by the ESD mechanism, a_{ESD} is the intercept and b_{ESD} the slope of the regression line relating offspring begging to parental provisioning (figure 1*b*) and e_{ESD} is the residual variation in offspring begging from the least-squares regression line (again assumed to be normally distributed with mean 0 and variance σ_x^2).

Equations (2.1) and (2.2) refer to linear regression equations where the original traits (measures of parental provisioning and offspring begging) have previously been standardized to $\sigma_x = 1$ and $\sigma_y = 1$. This is achieved by dividing the original individual trait values (x_i,y_i) by their standard deviation (σ_x,σ_y). As a consequence of this transformation, the standardized regression coefficients, i.e. the slopes of the lines describing the EDS and ESD mechanisms (b_{EDS} and b_{ESD}), are bound between -1 and 1 (Sokal & Rohlf 1995).

The intersection of the EDS and ESD regression lines corresponds to the proximate equilibrium, as envisaged by Hussell (1988). It is found for begging where the predicted level of provisioning from the EDS mechanism equals the level of provisioning from the ESD mechanism (figure 1*c*), i.e. where

$$\hat{y}_{\mathrm{EDS}} = y_{\mathrm{ESD}}. \qquad (2.3)$$

Prediction of provisioning levels from the EDS mechanism is straightforward following equation (2.1), but its determination from the ESD mechanism requires the inverse prediction (Sokal & Rohlf 1995) of equation (2.2). This is achieved by algebraically rearranging equation (2.2) for y_{ESD}:

$$y_{\mathrm{ESD}} = \frac{\hat{x}_{\mathrm{ESD}} - a_{\mathrm{ESD}} - e_{\mathrm{ESD}}}{b_{\mathrm{ESD}}}. \tag{2.4}$$

Substituting equations (2.1) and (2.4) into equation (2.3)

$$a_{\mathrm{EDS}} + b_{\mathrm{EDS}} x_{\mathrm{EDS}} + e_{\mathrm{EDS}} = \frac{\hat{x}_{\mathrm{ESD}} - a_{\mathrm{ESD}} - e_{\mathrm{ESD}}}{b_{\mathrm{ESD}}} \tag{2.5}$$

and solving for x (not considering the mechanism-indicating subscripts 'EDS' and 'ESD' of x) yields the equilibrium level of begging for individual families as follows:

$$x^* = \frac{a_{\mathrm{ESD}} + b_{\mathrm{ESD}} a_{\mathrm{EDS}} + e_{\mathrm{ESD}} + b_{\mathrm{ESD}} e_{\mathrm{EDS}}}{1 - b_{\mathrm{ESD}} b_{\mathrm{EDS}}}. \tag{2.6}$$

The asterisk denotes the value at equilibrium. The population mean equilibrium begging level, $\bar{x}^*$, is found by taking the expectation of equation (2.6), i.e. by setting the residuals e_{ESD} and e_{EDS} to 0, which reduces equation (2.6) to

$$\bar{x}^* = \frac{a_{\mathrm{ESD}} + b_{\mathrm{ESD}} a_{\mathrm{EDS}}}{1 - b_{\mathrm{ESD}} b_{\mathrm{EDS}}}. \tag{2.7}$$

The equilibrium point for parental provisioning is derived analogously, i.e. where the begging level predicted by the ESD mechanism equals the begging level from the EDS mechanism (figure 1*d*)

$$x_{\mathrm{EDS}} = \hat{x}_{\mathrm{ESD}}. \tag{2.8}$$

The intersection of the two regression lines (figure 1*d*) is found by substituting equation (2.2) and the inverse prediction of equation (2.1)

$$x_{\mathrm{EDS}} = \frac{\hat{y}_{\mathrm{EDS}} - a_{\mathrm{EDS}} - e_{\mathrm{EDS}}}{b_{\mathrm{EDS}}} \tag{2.9}$$

into equation (2.8)

$$\frac{\hat{y}_{\mathrm{EDS}} - a_{\mathrm{EDS}} - e_{\mathrm{EDS}}}{b_{\mathrm{EDS}}} = a_{\mathrm{ESD}} + b_{\mathrm{ESD}} y_{\mathrm{ESD}} + e_{\mathrm{ESD}}. \tag{2.10}$$

Solving for y (not considering the mechanism-indicating subscripts of y) yields

$$y^* = \frac{a_{\mathrm{EDS}} + b_{\mathrm{EDS}} a_{\mathrm{ESD}} + e_{\mathrm{EDS}} + b_{\mathrm{EDS}} e_{\mathrm{ESD}}}{1 - b_{\mathrm{ESD}} b_{\mathrm{EDS}}}. \tag{2.11}$$

Taking the expectation as before (setting e_{EDS} and e_{ESD} to 0) reduces equation (2.11) to

$$\bar{y}^* = \frac{a_{\mathrm{EDS}} + b_{\mathrm{EDS}} a_{\mathrm{ESD}}}{1 - b_{\mathrm{EDS}} b_{\mathrm{ESD}}}. \tag{2.12}$$

Equations (2.7) and (2.12) define the equilibrium levels of offspring begging and parental provisioning on the standardized scale. They can be transformed back to the original scales of offspring begging and parental provisioning by multiplying $\bar{x}^*$ by σ_x and $\bar{y}^*$ by σ_y, respectively.

3. DISCUSSION

The model presented here makes it possible to estimate quantitatively mechanisms and equilibria for begging and provisioning in a standardized way. It may also be used to translate units of offspring begging into units of parental provisioning, and vice versa, based on equations (2.6) and (2.11). Such conversions may be useful for testing the degree of fit between food demanded by begging and food actually provisioned (Kilner *et al.* 1999). Any significant misfit may indicate an ecologically, and maybe also evolutionarily, unstable state.

Critically, the regression equations (2.1) and (2.2), describing the EDS and ESD mechanisms, respectively, refer to causal regression equations (i.e. model I regressions; Sokal & Rohlf 1995) where the independent variable is manipulated experimentally. Purely observational studies will not be able to provide independent estimates of the two mechanisms (Hussell 1988).

The EDS mechanism may be investigated by exposing parents to various experimental levels of begging intensity (at least two levels when *assuming* linear effects), for example by using begging playback experiments and measuring the resulting parental provisioning. The ESD mechanism may be assessed by provisioning offspring experimentally with various levels of food (again, at least two) and measuring their begging levels. These experimental approaches have been widely used and are well established (Kilner & Johnstone 1997). New requirements for estimating equilibrium points for begging and provisioning following formulae (2.7) and (2.12) are that

(i) both mechanisms are studied at the same stage of offspring rearing and over the same time-span;
(ii) measurements of begging and provisioning are standardized before analysis;
(iii) the data are analysed by using linear regression analysis instead of the more widespread analyses of variance or *t*-tests approaches (see Kilner *et al.* (1999) for an example); and
(iv) provisioning measured in the EDS experiment and manipulated in the ESD experiment, and begging level measured in the ESD experiment and manipulated in the EDS experiment, respectively, are in equal units.

This fourth requirement is probably the most challenging. Ideally, the same food should be used for hand-feeding in the ESD experiment as is available to parents in the EDS experiment. This may be straightforward in mammals (i.e. milk) and in birds and insects kept in captivity, but it is less so in wild-living birds where the naturally provisioned food may not be known exactly. In addition, certain components of begging that may be measurable relatively easily are hard to manipulate directly (e.g. begging posture).

The estimated equilibria will reflect the components of provisioning and begging under investigation and the time-span over which the experiments are done. Currently, both playback and hand-feeding experiments have generally been carried out over just a few hours at most (but see Ottosson *et al.* 1997; Price 1998). Such estimates of mechanisms are important for understanding short-term behavioural dynamics in begging and provisioning, but may not accurately reflect the ultimately relevant mechanisms, expressed as the net EDS and ESD mechanisms over the total time that parents and their offspring interact. Current knowledge of EDS and ESD mechanisms is therefore potentially biased towards short-term provisioning responses by parents to sudden changes in begging, and towards short-term hunger-effects on begging. Longer-term effects potentially interfering with the short-term mechanisms, such as age-, competition- and/or condition-dependent (Price *et al.* 1996), learned (Kedar *et al.* 2000) and/or physiological and digestive (Clark 2002; Karasov & Wright 2002) adjustments, may often be excluded from the estimates. Each of these effects in isolation may be viewed as a 'partial' EDS or ESD mechanism causing short-term shifts in the equilibrium. The 'partial' mechanisms may combine to give the net EDS and ESD mechanisms and the resulting long-term equilibrium in potentially complex ways.

Extending the time-scale towards cross-generational effects, the model converges to a quantitative genetic description of mechanisms regulating parental provisioning and offspring begging through indirect genetic effects (Moore *et al.* 1997). The intercepts of the regression equations, a_{EDS} and a_{ESD}, become genotypic values for parental provisioning and offspring begging, respectively. The slope b_{ESD} corresponds to a maternal-effect coefficient (Kirkpatrick & Lande 1989) mediating the indirect genetic effect of provisioning on offspring begging, and b_{EDS} corresponds to an offspring-effect coefficient mediating the indirect genetic effect of begging on provisioning. A quantitative genetic model for general social interactions with reciprocal effects has derived a solution for trait expression that is formally equivalent to equations (2.7) and (2.12) (Moore *et al.* 1997). The formal equivalence of proximate equilibria for begging and provisioning (this model) and indirect-genetic-effect models (Moore *et al.* 1997) highlights the importance of time-scale in the interpretation of model parameters and equilibrium points. It also suggests that the model presented here may apply to general social interactions with reciprocal effects (if there are analogues to the EDS and ESD mechanisms).

The linear regression model described here may be a useful statistical tool especially in the study of the behavioural and evolutionary dynamics of offspring begging and parental provisioning. These areas are still poorly understood both empirically and theoretically (Royle *et al.* 2002). From an evolutionary viewpoint the partitioning of behavioural mechanisms into fixed baseline (a_{EDS}, a_{ESD}) and responsive (b_{EDS}, b_{ESD}) components suggests that variation in both the fixed and the responsive components may be involved in conflict resolution. There is thus the potential that families coevolve either towards flexible communicative resolutions, or towards rather rigid systems where communication plays a minor role. Evolutionary models for the resolution of family conflicts allowing EDS and ESD mechanisms to coevolve will be required to answer this question.

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