Behavioural attainability of evolutionarily stable strategies in repeated interactions

Ralph Dobler and Mathias Kölliker

University of Basel, Zoological Institute, Evolutionary Biology

Correspondence: R. Dobler, University of Basel, Zoological Institute, Evolutionary Biology, Vesalgasse 1, CH-4051 Basel, Switzerland (e-mail: ralph.dobler@stud.unibas.ch)

Word count: approx. 6200

Abstract

Theory for the evolution of social interactions based on continuous strategies often assumes for simplicity that expressed behaviours are independent from previous encounters. In reality, however, such dependencies are likely to be widespread and often strong, generating complex behavioural dynamics. To model this process and illustrate potential consequences for the evolution of behavioural interactions, we consider the behavioural dynamics of the interaction between caring parents and their demanding offspring, a prime example for long series of interdependent and highly dynamic interactions. These dynamics can be modelled using functions describing mechanisms for how parents and their offspring respond to each other in the interaction. We establish the general conditions under which the behavioural dynamics converge towards a proximate equilibrium and refer to such converging interactions as behaviourally stable strategies (BSSs). We further demonstrate that there is scope for behavioural instability under realistic conditions; that is, whenever parents and/or offspring 'overreact' beyond some threshold. By applying the derived condition for behavioural stability to evolutionary models of parent-offspring conflict resolution, we show by numerical simulations that evolutionarily stable strategies (ESSs) of current models are not necessarily behaviourally stable. Because behavioural instability implies that expressed levels of behaviours deviate from the ESS, behavioural stability is required for strict evolutionary stability in repeated behavioural interactions.

Key words: behavioural dynamics; ESS; game theory; interacting phenotypes; parent-offspring conflict; social interaction

Conspicuous offspring behaviours and displays to demand resources from their parents can be observed in most animal species with parental care (Clutton-Brock 1991). According to parent-offspring conflict (POC) theory, offspring are usually selected to demand more resources from their parents than the parents should provide (Trivers 1974). This phenomenon can be evolutionarily explained in terms of the outcome of the POC over resource distribution, where offspring begging and parental provisioning strategies reflect an evolved resolution of this conflict (Trivers 1974; Parker 1985; Godfray 1995; Kilner & Johnstone 1997; Mock & Parker 1997; Royle et al. 2002). There are two main types of game-theoretic approaches to modelling conflict resolution. The 'scramble competition' model assumes that offspring control parental food allocation (Parker & Macnair 1979; Parker 1985; Parker et al. 2002). The 'honest signalling' model assumes, that parents control food allocation (Godfray 1991; Godfray & Johnstone 2000). Both types of models can explain the evolution of condition-dependent, conspicuous and costly offspring begging and parental response.

These models generally assume for simplicity a single interaction, or equivalently multiple independent interactions, between parent and offspring (Maynard-Smith 1982; Parker 1985; Houston et al. 1988; Godfray 1999; McNamara et al. 1999; Godfray & Johnstone 2000; Royle et al. 2002; but see Johnstone 1996 for a two-step exception) and the evolving strategies are taken to be adequately represented by the behavioural outcome of a one-off interaction. However, in reality the interactions between parents and offspring are behaviourally very dynamic and typically involve repeated encounters that are interdependent (McNamara et al. 1999; Godfray & Johnstone 2000). The issue of stability has been thoroughly explored in conflict resolution models from the perspective of

3

evolutionary stability (e.g. Takada & Kigami 1991; Rodríguez-Gironés et al. 1998; McNamara et al. 1999). But it is not known whether, and under what conditions, the behavioural dynamics of repeated parent-offspring interactions allow the behaviours actually to be expressed according to the idealized strategies in the evolutionary models.

Here, we model the repeated parent-offspring interaction using a behavioural reaction norm approach (Smiseth et al. 2008) in an expanded negotiation model framework (Moore et al. 1997; McNamara et al. 1999; Taylor & Day 2004; Johnstone & Hinde 2006), where a demand function defines how offspring adjust their begging to variation in parental provisioning, and a supply function defines how parents adjust their provisioning to variation in offspring begging (Fig. 1; Hussell 1988). These functions define how parents and offspring react to each other, and the resulting dynamics can be considered as a negotiation process. Under this perspective, evolutionary strategies can be represented by the slopes and/or shapes of these functions, mediate the behavioural dynamics of the interaction (Smiseth et al. 2008). In his graphical model, Hussell (1988) focussed on the expected behavioural equilibrium over multiple interdependent parent-offspring interactions (see also Kölliker 2003). This equilibrium represents the behavioural strategies considered in the game theoretic conflict resolution (Godfray 1991; Mock & Parker 1997; Parker et al. 2002) and quantitative genetic coadaptation models (Wolf & Brodie 1998; Kölliker et al. 2005). However, given a pair of supply and demand functions, the behavioural dynamics of the repeated parent-offspring interactions may, or may not, lead to this equilibrium. Thereby, the shapes of the supply and demand functions affect the stability of the behavioural equilibrium (Samuelson 1976). Understanding the conditions under which

4

the behavioural equilibrium is actually reached in the interaction is critical,

because only a stable behavioural equilibrium can adequately represent

strategies in current evolutionary resolution models (see Samuelson 1976

for an economical context).

We provide a formal model and results from numerical analyses exploring

the stability of behavioural equilibria and behavioural strategies in

parent-offspring interactions for different shapes of supply and demand

functions. We also show for a range of realistic conditions that current

conflict resolution models predict evolutionarily stable strategies (ESSs)

that are behaviourally not stable.

The Model

Behavioural equilibria

The offspring behavioural reaction norm for demand (Taylor & Day 2004;

Smiseth et al. 2008) is defined by the demand function $D = f(S)$,

describing the dependence of offspring begging on parental provisioning.

The parental behavioural reaction norm for supply (Taylor & Day 2004;

Smiseth et al. 2008) is defined by the supply function $S = g(D)$, describing

the dependence of parental provisioning on offspring begging. The

interdependence of the two recursive functions can be used to model the

behavioural dynamics over repeated interactions of parents and offspring

(Fig. 1).

To display and formalize this feedback and find the behavioural

equilibrium, the arguments of the two functions need to be expressed in the

5

same currency. This can graphically be achieved by inverting the supply

function and superimposing it on the demand function (Hussell 1988). The

intersection point of the two functions represents the behavioural

equilibrium. Formally, the behavioural equilibrium is derived by inverting

the supply function, setting it equal to the demand function:

$$f(S_{eq}) = g^{-1}(S_{eq}).$$

Then solving for S_{eq}, where S_{eq} is the equilibrium value for the supply and

setting S_{eq} in the demand function yields the equilibrium value for demand

D_{eq} (Kölliker 2003).

Stability of behavioural equilibria

To address the behavioural stability of the equilibria, the dynamics of

parent and offspring behaviours over repeated interactions need to be

explored explicitly. Only when repeated parent-offspring interactions

converge towards the equilibrium, the equilibrium and the strategies are

behaviourally stable (Fig. 1a). At such an equilibrium we refer to the pairs

of strategies as behaviourally stable strategies (BSSs), represented by the

slopes and/or shapes of the supply and demand functions. When repeated

parent-offspring interactions diverge away from the equilibrium, the

equilibrium and the strategies are behaviourally not stable (Fig. 1b). We

used the standard mathematical techniques based on discrete-time

dynamics to address the stability of behavioural equilibria (Otto & Day

2007, pp. 163 - 169). In our model, discrete time steps are from one

specific interaction (offspring demands, parent provides) to the next and

136 the process is started with an offspring begging event.

137 Our model in principle explores a behavioural negotiation process between
138 parents and offspring (e.g. McNamara et al. 1999; Taylor & Day 2004;
139 Johnstone & Hinde 2006) in which parent and offspring interact according
140 to their behavioural reaction norms. In contrast to previous models (e.g.
141 McNamara et al. 1999; Taylor & Day 2004; Johnstone & Hinde 2006), we
142 focus on the behavioural process and allow for asymmetric functions, as we
143 have parental supply and offspring demand in our model, which are
144 represented by response mechanisms for different kinds of behaviour.

145 ## *Numerical analyses*

146 To further explore the behavioural dynamics of parent-offspring
147 interactions explicitly, we also used numerical simulations for the changes of
148 demand (begging) level and supply (provisioning) level over a series of 2000
149 time steps for a given set of supply and demand functions (Fig. 1). For the
150 first time step the initial demand level D_0 was given and for subsequent
151 steps the value of the supply function was used as argument of the demand
152 function and vice versa. The initial demand level was randomly chosen
153 within 10% around the equilibrium D_{eq}. This choice increased the
154 likelihood of reaching the equilibrium with 2000 interactions even when the
155 process of convergence was slow. But any initial demand level could have
156 been chosen. There was no effect of initial condition on the outcome
157 (stability/instability) of the interaction (see Results). Values for supply
158 and demand were represented on a standardized scale from 0 (minimum) to
159 1 (maximum). The functions we used for supply and demand were strictly
160 monotonic (see below). A maximum level of demand was set at the point of

7

no supply, resulting in intercepts of 1 for the demand function and 0 for the

supply function. The interactions between parents and offspring were

assumed to be error free. That is, the dynamics of the behavioural

interaction strictly followed the supply and demand functions without any

deviation. For simplicity we assumed a single offspring interacting with a

single parent (Hussell 1988; Godfray 1991; Kölliker et al. 2005).

Specific function types

We numerically investigated the impact of two different types of functions

on behavioural stability. Linear functions are the simplest and usual way to

represent the parent-offspring interaction. They are standard in

quantitative genetic maternal effect (Kirkpatrick & Lande 1989) and

coadaptation models (Wolf & Brodie 1998; Kölliker 2003; Kölliker et al.

2005), and reflect the local gradients in game-theoretic conflict resolution

models (Godfray 1991; Parker et al. 2002). In addition, to simulate the

consequences of slightly more complex responses on the behavioural

dynamics, we used power functions (Smiseth et al. 2008), for which the

slopes are not constant but change with the level of supply and demand.

This may have important consequences for the behavioural dynamics and

stability of the parent-offspring interaction.

In the linear case, the supply function was defined as $S = g(D) = aD + y$,

with slope a and intercept $y = 0$ (Fig. 2a). The demand function was

defined as $D = f(S) = bS + x$, with slope b and intercept $x = 1$ (Fig. 2b).

The intercepts reflect the previously mentioned assumption of maximal

begging in the absence of provisioning. The slopes a of the supply function

could vary between zero and infinity ($0 < a < \infty$) and the slopes b for the

8

186 demand function between minus infinity to zero ($-\infty < b < 0$).

187 In the case of power functions, the supply function was defined as

188 $S = g(D) = 1 - (1 - D)^k$ (Fig. 2c) and the demand function was defined as

189 $D = f(S) = (1 - S)^l$ (Fig. 2d). The parameters k and l define the

190 corresponding strength and direction of the curvature and could both range

191 from zero to infinity ($0 < k < \infty$, $0 < l < \infty$).

Numerical application to ESS models

193 The link between behavioural dynamics and evolutionary stability was

194 explored by applying our BSS condition to an already existing ESS model

195 in a numerical sensitivity analysis. We chose the scramble competition

196 resolution model, for which the role of supply and demand functions has

197 been made explicit (Parker 1985; Mock & Parker 1997; Parker et al. 2002).

198 But our analysis in principle also applies to honest signalling models

199 (Godfray 1991; Godfray & Johnstone 2000), although this is based on a

200 different (i.e. additive rather than multiplicative) fitness model. Scramble

201 competition models assume that parents have a fixed quantity of resources

202 available for reproduction. A unit of investment in a given offspring

203 enhances that offspring's survival chances, but at the expense of other

204 offspring the parent can produce. Offspring survival chances follow a curve

205 of diminishing returns with respect to the parental resources obtained

206 (Smith & Fretwell 1974; Parker 1985). Further, for evolutionary stability,

207 offspring begging has to be costly. For simplicity, we assume that offspring

208 survival decreases linearly with increased begging (Parker et al. 2002). To

209 allow direct comparison with the evolutionary model, the dimensionless

210 level of supply in our behavioural model can be interpreted in units of

9

211 parental investment.

212 The scramble competition ESS is defined via the local gradients of supply

213 and demand functions at the ESS (Parker 1985; Mock & Parker 1997; see

214 Appendix), which are parameters in the model and assumed to be

215 nonevolving. We carried out a broad numerical sensitivity analysis, varying

216 the gradients (i.e. the slopes) of the supply and demand functions and the

217 parameters p and q of the associated cost and benefit functions of begging

218 and provisioning, respectively (see Parker et al. 2002 and Appendix for

219 details of the functions), to test for the behavioural stability of the ESS for

220 specific sets of supply and demand functions (with known slopes and

221 intercepts) and, hence, whether they are BSSs or not.

222 To explore numerically the parameter space of the scramble competition

223 ESSs for converging behavioural dynamics we performed the following

224 steps: 1) We generated a behavioural equilibrium grid for the supply and

225 demand function pairs (1'000'000 behavioural equilibria; 1'000 demand

226 levels and 1'000 supply levels, evenly distributed) in the parameter range of

227 our model. 2) We calculated the ESSs according to the scramble

228 competition model (Parker & Macnair 1979; Parker 1985; Parker et al.

229 2002) in terms of a demand and supply function pairs (according to Eqs

230 A-2 and A-3). 3) For all of these function pairs we checked whether the

231 intercept of the demand function was close to 1 and that for the supply

232 function close to 0 to fulfil the assumptions we made to derive the BSS

233 conditions. Intercepts were deemed close enough when they deviated by less

234 than 0.005. 4) The equilibria of those funtion pairs which satisfied these

235 criteria were matched to the behavioural equilibrium grid generated before

236 (see step 1). We took the numerical values for the behavioural equilibrium

237 and the evolutionary equilibrium to be equal when they were within a

238 margin of ± 0.001, which corresponds to the resolution of the behavioural

239 equilibrium grid. 5) In cases where we found more than one function pair

240 that numerically satisfied our matching conditions, we chose the one with

241 the smallest mismatch to be the 'true' one, as we expected only one ESS

242 per parameter combination p and q. Choosing another pair did not alter

243 the final result (i.e. whether an ESS was behaviourally stable or not). 6)

244 For the slope combinations where behavioural and evolutionary equilibrium

245 matched, we checked whether or not the equilibrium was also behaviourally

246 stable. For this we applied the stability conditions of our formal model.

247 We ran our model for 90 different fitness parameter value combinations p

248 and q in the cost and benefit functions of the scramble competition model

249 (see Parker et al. 2002 and Appendix for details of the functions).

250 Variation in these fitness parameters may have an impact on the outcome

251 of the behavioural stability of the POC resolution, because different slopes

252 for demand and supply functions are required to reach the ESS.

253 We used R version 2.4.0 (2006-10-03) and Mathematica 6.0.1.0 for the

254 analyses and simulations (R Development Core Team 2006; Wolfram

255 Research, Inc. 2007).

Results

Stability of behavioural equilibria and numerical analyses

258 We calculated the stability index λ following Otto & Day (2007) for

259 discrete-time dynamics systems. λ allows us to determine if a dynamic

system that is close to an equilibrium converges towards, or diverges away from, this equilibrium from one time-step to the next. In our case, it is the derivative of the function describing the begging level at the next time step, which is a combination of the supply and demand function. In our model this is

$$\lambda = f'(S_n),$$

where $f(S_n) = D_{n+1}$ is the begging level after one interaction when starting at D_n, with

$$D_{n+1} = f(S_n) = f(g(D_n)).$$

S_n is the supply level and $f(S_n)$ the demand function. $f(g(D_n))$ is again the demand function, expressed as a function of the demand level one interaction before. The resulting value for λ is

$$\lambda = f'(S_n) = f'(g(D_n))g'(D_n) = f'(S_n)g'(D_n).$$

(Note that $g(D_n) = S_n$).

For linear demand and supply functions we get

$$f(S_n) = D_{n+1} = b(aD_n + y) + x,$$

where x and y are the intercepts of the demand and supply function, respectively. And for λ we get

$$\lambda = ab.$$

A value of λ between -1 and 1 indicates a stable dynamic equilibrium
(Otto & Day 2007). So the general stability condition for the behavioural
interaction between a parent and its offspring is

$$\lambda = |ab| < 1. \tag{1}$$

For the case of linear supply and demand functions, this condition is for
local and global stability; it is not only valid at/near the equilibrium but
for any initial begging level D_n, because the functions involved are linear
and the slopes a and b apply over the whole range. This stability condition
can also be proven by using the convergence criteria for infinite repeated
interactions between parent and offspring (see Appendix).

Numerical simulations

Our numerical simulations deal only with a subset of all possible functions,
namely a supply function with a positive slope a (parent increases supply
level with increasing demand level) and a demand function with a negative
slope b (offspring decreases demand level with increasing supply level) (Figs
2a and b). This assumption is also made in scramble competition models
(Parker et al. 2002). The stability condition under these assumptions and
for linear supply and demand functions is

$$-1 < ab < 0.$$

13

291 This solution is a partial solution of the conditions for general stability

292 derived earlier (Eq. 1), confirming the result of our formal model. The

293 product of the two parameters a and b defines the behavioural stability of

294 linear parent-offspring interactions. When ab has a value between -1 and 0

295 ($-1 < ab < 0$), then the repeated interactions of parent and offspring

296 converge towards the equilibrium and reflect a BSS. In all these cases the

297 two functions intersect at a demand level between 0.5 and 1

298 ($0.5 < D_{eq} < 1$, Fig. 3a), under the assumptions of our model (i.e. slopes of

299 the functions are of opposite sign and the intercepts are 0 and 1,

300 respectively). The threshold level of 0.5 can be derived analytically (see

301 Appendix, A-1). That half of the function pairs that intersect above a

302 demand level of 0.5 represent a BSS. The half of the function pairs that

303 intersect below a demand level of 0.5 represent behaviourally not stable

304 strategies, resulting in divergence of the behavioural interaction.

305 For the power functions (Figs 2c and d), the local stability conditions

306 follow the general rule

$$-1 < f'(S_{eq})g'(D_{eq}) < 1. \qquad (2)$$

307 $f'(S_{eq})$ is the derivative (local gradient) of the demand function at the

308 equilibrium and $g'(D_{eq})$ is the derivative of the supply function at the

309 equilibrium.

310 According to the results of our simulation, this stability condition seems

311 not only valid at the equilibrium but over the whole value range of possible

312 initial demand levels (data not shown). So we can state the general

313 stability conditions for the power functions within the value range of our

14

numerical simulation as follows:

$$-1 < f'(S)g'(D) < 0.$$

This is equivalent to the stability condition for linear functions, but generalized to the case of non-linear power functions. The behavioural stability of the parent-offspring interaction depends only on the derivatives (the slopes) of the describing functions of demand and supply. Again, under the assumptions of our model, all supply and demand function pairs that intersect at a level of demand between 0.5 and 1 ($0.5 < D_{eq} < 1$) have a behaviourally stable equilibrium (Fig. 3b), whereas those that intersect between 0 and 0.5 ($0 < D_{eq} < 0.5$) do not.

Numerical application to ESS models

For 17 out of the 90 simulations the ESS was outside the considered parameter space or the intercepts deviated too much from 1 (for the demand function) or 0 (for the supply function). For 73 simulations we found ESSs inside the considered parameter space where the intercepts of the functions matched to 1 and 0, respectively. For 16 cases the difference between ESS and BSS was larger than our matching criteria (i.e. the difference in either demand level or supply level was larger than 0.001 (our grid resolution) and the function pair could hence not be clearly assigned to one grid point). Out of the remaining 57 cases where the intercepts fulfilled our matching criteria, 33 turned out to be behaviourally stable (BSS) and 24 were behaviourally not stable (Table 1).

ESSs were behaviourally stable in the lower range of explored begging costs

(*q* ranging from -0.1 to -0.35), representing higher numerical values for ESS levels of demand. For higher begging cost parameter values, and the correspondingly lower values for ESS levels of demand, the ESSs were behaviourally not stable. The parameter p, determining the benefit of parental supply for offspring survival, was not associated with behavioural stability (Table 1).for the begging cost parameter predicted ESSs that are also BSSs, and higher values for the begging cost parameter lead to predicted ESSs that are behaviourally not attainable (Table 1).

Discussion

Behavioural interactions based on continuous strategies generate complex dependencies and behavioural dynamics over time, raising the question of behavioural stability. To define a condition for behavioural stability in repeated interactions we proposed the novel concept of the behaviourally stable strategy (BSS): a BSS is characterized by behavioural dynamics of repeated interactions that converge towards the behavioural equilibrium. While the BSS is a proximate condition for the outcome of behavioural interactions, it has repercussions on evolutionary stability in a stricter sense. Non converging behavioural dynamics imply deviation from the expressed behavioural levels that would represent the ESS. Thus, by definition, behaviourally unstable strategies lead to deviation from the single-interaction or negotiation ESS (see below) and to corresponding fitness penalties. To illustrate this argument further, we have shown by simulations that there are realistic conditions under which ESSs for parent-offspring conflict resolution are behaviourally not stable. While this analysis is based on scramble competition resolution models (Parker et al.

16

2002), in principle the same basic conclusion apply to honest signalling models (Godfray 1991) because neither type of model incorporates the dynamics of repeated interactions.

Negotiation models (McNamara et al. 1999; Taylor & Day 2004; Johnstone & Hinde 2006) and quantitative genetic models of interacting phenotypes (Moore et al. 1997; Kölliker 2003) both assume $|\lambda|$ to be smaller than 1 and thereby ensure behavioural stability in the predicted evolutionary outcomes. Our model provides the biological rationale for this critical assumption in negotiation and interacting phenotype models.

Behavioural stability

The behavioural stability of parent-offspring interactions at the equilibrium depends only on the derivatives (the change rates) of the supply and demand function. The absolute value of the product of the two derivatives has to be smaller than 1 (Eq. 2). Samuelson (1941, 1976) found analogous results for linear demand and supply functions in economics for the equilibrium prices of products. This result can be biologically interpreted such that the stability condition is likely to be violated when at least one interactant reacts too sensitively (i.e. it 'overreacts') to a behavioural change in the other interactant, leading to unsteady (oscillating) dynamics.

Under the assumptions of an intercept of 0 for the supply and of 1 for the demand function, the equilibrium is behaviourally stable for linear response functions as well as for power response functions, when the begging level at the equilibrium is larger than 0.5 (i.e. generally speaking the average

17

between the minimum and maximum level, see Appendix). We present the

derivation for the linear case, although an equivalent solution can be shown

for power functions (G. Nöldeke, personal communication; R. Dobler and

M. Kölliker, unpublished results)

The increased complexity in the response functions from a linear to a

power function had no impact on the outcome of the behavioural stability

in our simulations. Nevertheless, we cannot reject the possibility that

response functions with a more elaborate complexity (e.g. logistic

functions, quadratic functions or higher order functions) may influence the

behavioural stability, including the possibility of multiple alternative

behavioural equilibria (i.e. more than one intersection point). In such more

complex cases the stability may not only depend on the response functions

and their derivatives but also on the starting conditions, adding another

level of complexity to the model. For such models it would not only be

interesting to find stability conditions but also to find possible conditions

and circumstances that allow the interaction to change from one

behavioural equilibrium to another. Under such more complex conditions,

behaviourally stable equilibria may not always be attainable.

Communication errors and shifting response functions (e.g. due to changing

environmental conditions or offspring age) may make the behavioural

equilibrium shift over time, which would constantly reintroduce behavioural

dynamics, likely rendering even stronger the expected selection pressure on

behavioural reaction norms that allow fast behavioural convergence. In

future models it would be interesting to incorporate perception errors, time

lags and developmental/plastic function adjustments (Johnstone & Grafen

1992; Johnstone 1994), and to study such plasticity in experimental work

18

(e.g. Hinde & Kilner 2007). Such inclusions would add realism and specificity to the model, but our major conclusion that the behavioural dynamics need to be addressed for an understanding of evolved strategies in repeated social interactions will most likely not be affected.

So far, empirical studies on behavioural dynamics mainly focused on the average effect which a change in behaviour (experimental or natural) of an interactant has on the behaviour of another interactant (e.g. Smith et al. 1988; Kilner 1995; Ottosson et al. 1997; Kilner et al. 1999). Although these studies give valuable insight on the overall adjustment (change rate) and plasticity of behaviour s, they do not address the underlying dynamics leading to the observed behavioural outcome. Experiments where a supposedly equilibrated system is deviated temporarily and the subsequent interaction-to-interaction dynamics analysed explicitly could provide the data required to determine to what degree a behavioural reaction norm (i.e. response rule) approach can actually be used to model the behavioural dynamics in repeated interactions (Roulin 2002; Hinde & Kilner 2007; Smiseth et al. 2008). Behaviourally stable strategies (BSSs) are expect to stabilise back to the initial equilibrium after the temporary disturbance.

Application of the BSS concept

Applying our BSS model to scramble competition resolution models (Parker 1985; Mock & Parker 1997; Parker et al. 2002) confirms that predicted ESSs of single-interaction models are not necessarily behaviourally stable strategies. Some are either outside the parameter range or they represent a behaviourally unstable equilibrium. In both cases, what would be the ESS can behaviourally never be reached,

19

regenerating selection in the interactions. Under the specific conditions of the chosen intercepts, and from a perspective of behavioural stability, intermediate to high begging levels should be favoured over the course of selection, because only these can be the result of convergent behavioural dynamics. This may appear counterintuitive at first sight, as one would associate higher begging levels with increased costs, which should be evolutionarily unfavourable (Moreno-Rueda 2007). However, higher begging costs also imply lower evolved begging levels at the ESS (Parker 1985; see Appendix) and when ESS begging levels exceed the level for behavioural stability, instability ensues (Table 1). Thus, there are behavioural stability constraints in parent-offspring interactions, which would favour evolutionary conflict resolutions with relatively high levels of begging and, hence, relatively low associated begging costs. In addition to the well-studied selection for optimal conflict resolution, we suggest selection on behavioural reaction norms that enhance the likelihood for behaviourally stable repeated interactions.

Conclusions

The importance of behavioural stability is not restricted to the functional context of parent-offspring interactions, but may include any context where fast-responding short-term interactions are involved (e.g. dominance interactions (Matsumura & Kobayashi 1998), biological markets (Noe & Hammerstein 1994, 1995), cell interactions (Hofmeyr & Cornish-Bowden 2000), negotiation over care (McNamara et al. 1999; Taylor & Day 2004; Johnstone & Hinde 2006)).

There are usually many BSSs that are not an ESS. Many interactions

20

behaviourally converge but yield behavioural levels with suboptimal fitness consequences. This is not surprising, since behavioural stability alone tells us nothing about fitness. More revealing are the cases where a predicted ESS (in terms of a pair of slopes for the supply and demand reaction norms) is not a BSS. We could show for the scramble competition model (Parker 1985; Mock & Parker 1997; Parker et al. 2002) that behaviourally unstable ESSs are predicted when begging costs are of greater than some intermediate level. BSS and ESS are two conditions to evaluate the stability of repeated interactions that deal with the proximate and ultimate dimension of repeated interactions, respectively. Both need to be met for evolutionary stability in a stricter sense.

Acknowledgments

Appendix

Alternative proof of the behavioural stability conditions for

linear behavioural reaction norms

480 The change in begging over one time step is

$$D_{n+1} = b(aD_n + y) + x.$$

481 The change of begging level over n time steps is therefore

$$D_n = a^n b^n D_0 + a^{n-1} b^n y + a^{n-1} b^{n-1} x + a^{n-2} b^{n-1} y + a^{n-2} b^{n-2} x + ... + abx + by + x.$$

482 Factoring out $a^i b^i$ for $0 \leqslant i \leqslant (n-1)$ leads to

$$D_n = a^n b^n D_0 + (x + yb) \sum_{i=0}^{i=n-1} a^n b^n.$$

483 The second term on the right hand side is a geometric series that for

484 $n \to \infty$ only converges, when $|ab| < 1$. For this case ($|ab| < 1$) the first

485 term on the right hand side converges to 0. From this we can conclude that

486 the repeated interaction only converges towards the equilibrium (D_{eq})

487 when $|ab| < 1$. Otherwise the interaction diverges.

488 The demand level at the equilibrium D_{eq} (for $|ab| < 1$) is:

$$D_{eq} = \lim_{n \to \infty} a^n b^n D_0 + (x + yb) \sum_{i=0}^{i=n-1} a^n b^n = \frac{x + yb}{1 - ab}.$$

489 For the linear case in our simulation we have $x = 1$ and $y = 0$, resulting in

$$D_{eq} = \frac{1}{1 - ab}. \qquad \text{(A-1)}$$

490 This proves that the behavioural equilibrium is only stable if and only if

491 $D_{eq} > 0.5$ (because $|ab| < 1$).

492 More generally, the threshold level for stability/instability D_{eq} for any

493 intercepts x and y is

$$D_{eq} = \frac{x + y}{1 - ab} = \frac{x + y}{2}.$$

494 Because $1 - ab < 2$, the lowest value for D_{eq} is the mean of the two

495 intercepts x and y, representing the threshold demand level for BSS.

Details of the scramble competition model

497 Following Mock & Parker (1997) and Parker et al. (2002), we used the

498 following functions for cost and benefit. For the costs of begging we used

499 the survival probability κ:

$$\kappa(D) = pD + 1,$$

500 with p as the parameter (slope) for the cost of begging ($-1 < p < 0$) and

501 an intercept of 1. As the costs reduce the net benefit, the intercept of 1

502 indicates no costs when there is no begging. Values of p close to 0 indicate

503 a weak begging cost which becomes higher the more p diverges from 0.

504 With $p = -1$, maximal begging results in a survival probability of 0. For

24

505 the benefit (μ) of supply we used

$$\mu(S) = 1 - e^{-q(S-0.1)},$$

506 with the parameter q for the benefit of supply bigger than 0 ($q > 0$).

507 Applying these functions to the ESS conditions of the scramble

508 competition model (Parker 1985, Eqs 2 and 3; Mock & Parker 1997) with

$$\beta = \frac{0.5v}{v - 1}$$

509 for the case of 'true monogamy' (see Parker 1985) and

$$\alpha + \beta = 1.$$

510 α and β are coefficients assigned to special levels of sib competition,

511 parental care and mating system. v is the product of the two gradients of

512 the supply and demand functions (Parker et al. 2002)

$$v = g'(D_{eq})f'(S_{eq}).$$

513 This leads to

$$D_{ESS} = \beta \frac{\kappa(D_{ESS})}{\kappa'(D_{ESS})} = \left(\frac{0.5ab}{ab - 1} \right) \frac{pD_{ESS} + 1}{D_{ESS}} \tag{A-2}$$

514 as the stability condition for demand and

$$S_{ESS} = \alpha \frac{\mu(S_{ESS})}{\mu'(S_{ESS})} = \left(1 - \frac{0.5ab}{ab-1}\right) \frac{1 - e^{-q(S_{ESS}-0.1)}}{e^{-q(S_{ESS}-0.1)}k} \qquad \text{(A-3)}$$

515   as the stability conditions for supply. This are the two strategies offspring

516   and parents, respectively, should play to solve the POC from an

517   evolutionary perspective.

518   Note: v (see Parker et al. 2002) is equivalent to λ in our condition for

519   behavioural stability.

References

Clutton-Brock, T., 1991. The evolution of parental care. Monographs in Behavior and Ecology. Princeton University Press, Princeton, New Jersey.

Godfray, H. C. J., 1991. Signaling of need by offspring to their parents. *Nature* **352**, 328–330.

Godfray, H. C. J., 1995. Evolutionary theory of parent-offspring conflict. *Nature* **376**, 133–138.

Godfray, H. C. J., 1999. Parent-offspring conflict. In: Levels of selection in evolution (ed. L. Keller), pp. 100–120. Monographs in behavior and ecology Princeton University Press, Princeton, New Jersey.

Godfray, H. C. J. & Johnstone, R. A., 2000. Begging and bleating: the evolution of parent-offspring signalling. *Philosophical Transactions of the Royal Society of London Series B* **355**, 1581–1591.

Hinde, C. A. & Kilner, R. M., 2007. Negotiations within the family over the supply of parental care. *Proceedings of the Royal Society of London Series B* **274**, 53–60.

Hofmeyr, J. H. S. & Cornish-Bowden, A., 2000. Regulating the cellular economy of supply and demand. *FEBS Letters* **476**, 47–51.

Houston, A., Clark, C., McNamara, J., & Mangel, M., 1988. Dynamic-models in behavioral and evolutionary ecology. *Nature* **332**, 29–34.

Hussell, D. J. T., 1988. Supply and demand in tree swallow broods: a

model of parent-offspring food provisioning interactions in birds. *American Naturalist* **131**, 175–202.

Johnstone, R. A., 1994. Honest signaling, perceptual error and the evolution of all-or-nothing displays. *Proceedings of the Royal Society of London Series B* **256**, 169–175.

Johnstone, R. A., 1996. Begging signals and parent-offspring conflict: do parents always win? *Proceedings of the Royal Society of London Series B* **263**, 1677–1681.

Johnstone, R. A. & Grafen, A., 1992. The continuous Sir Philip Sidney game: a simple-model of biological signaling. *Journal of Theoretical Biology* **156**, 215–234.

Johnstone, R. A. & Hinde, C. A., 2006. Negotiation over offspring care - how should parents respond to each other's efforts? *Behavioral Ecology* **17**, 818–827.

Kilner, R., 1995. When do canary parents respond to nestling signals of need. *Proceedings of the Royal Society of London Series B* **260**, 343–348.

Kilner, R. & Johnstone, R. A., 1997. Begging the question: are offspring solicitation behaviours signals of needs? *Trends in Ecology and Evolution* **12**, 11–15.

Kilner, R. M., Noble, D. G., & Davies, N. B., 1999. Signals of need in parent-offspring communication and their exploitation by the common cuckoo. *Nature* **397**, 667–672.

Kirkpatrick, M. & Lande, R., 1989. The evolution of maternal characters. *Evolution* **43**, 485–503.

28

567 **Kölliker, M.**, 2003. Estimating mechanisms and equilibria for offspring
568 begging and parental provisioning. *Proceedings of the Royal Society of*
569 *London Series B* **270**, S110–S113.

570 **Kölliker, M., Brodie, E. D., & Moore, A. J.**, 2005. The coadaptation
571 of parental supply and offspring demand. *American Naturalist* **166**,
572 506–516.

573 **Matsumura, S. & Kobayashi, T.**, 1998. A game model for dominance
574 relations among group-living animals. *Behavioral Ecology and*
575 *Sociobiology* **42**, 77–84.

576 **Maynard-Smith, J.**, 1982. Evolution and the theory of games.
577 Cambridge University Press, Cambridge, UK.

578 **McNamara, J. M., Gasson, C. E., & Houston, A. I.**, 1999.
579 Incorporating rules for responding into evolutionary games. *Nature* **401**,
580 368–371.

581 **Mock, D. & Parker, G.**, 1997. The evolution of sibling rivalry. Oxford
582 Series in Ecology and Evolution. Oxford University Press, Oxford, UK.

583 **Moore, A. J., Brodie, E. D., & Wolf, J. B.**, 1997. Interacting
584 phenotypes and the evolutionary process. 1. direct and indirect genetic
585 effects of social interactions. *Evolution* **51**, 1352–1362.

586 **Moreno-Rueda, G.**, 2007. Is there empirical evidence for the cost of
587 begging? *Journal of Ethology* **25**, 215–222.

588 **Noe, R. & Hammerstein, P.**, 1994. Biological markets supply and
589 demand determine the effect of partner choice in cooperation, mutualism
590 and mating. *Behavioral Ecology and Sociobiology* **35**, 1–11.

591 **Noe, R. & Hammerstein, P.**, 1995. Biological markets. *Trends in*
592 *Ecology and Evolution* **10**, 336–339.

593 **Otto, S. P. & Day, T.**, 2007. A biologist's guide to mathematical
594 modeling in ecology and evolution. Princeton University Press,
595 Princeton, New Jersey.

596 **Ottosson, U., Bäckman, J., & Smith, H. G.**, 1997. Begging affects
597 parental effort in the pied flycatcher, Ficedula hypoleuca. *Behavioral*
598 *Ecology and Sociobiology* **41**, 381–384.

599 **Parker, G. A.**, 1985. Models of parent-offspring conflict. 5. effects of the
600 behavior of the two parents. *Animal Behaviour* **33**, 519–533.

601 **Parker, G. A. & Macnair, M. R.**, 1979. Models of parent-offspring
602 conflict. 4. suppression evolutionary retaliation by the parent. *Animal*
603 *Behaviour* **27**, 1210–1235.

604 **Parker, G. A., Royle, N. J., & Hartley, I. R.**, 2002. Intrafamilial
605 conflict and parental investment: a synthesis. *Philosophical Transactions*
606 *of the Royal Society of London Series B* **357**, 295–307.

607 **R Development Core Team**, 2006. R: A language and environment for
608 statistical computing. R Foundation for Statistical Computing, Vienna,
609 Austria. ISBN 3-900051-07-0, http://www.R-project.org.

610 **Rodríguez-Gironés, M. A., Enquist, M., & Cotton, P. A.**, 1998.
611 Instability of signaling resolution models of parent-offspring conflict.
612 *Proceedings of the National Academy of Sciences, U.S.A.* **95**, 4453–4457.

613 **Roulin, A.**, 2002. The sibling negotiation hypothesis. In: The evolution of
614 begging: competition, cooperation and communication (eds. J. Wright &
615 M.L. Leonard), pp. 107–126. Springer, Berlin.

616 **Royle, N. J., Hartley, I. R., & Parker, G. A.**, 2002. Begging for
617   control: when are offspring solicitation behaviours honest? *Trends in*
618   *Ecology and Evolution* **17**, 434–440.

619 **Samuelson, P. A.**, 1941. The stability of equilibrium: comparative statics
620   and dynamics. *Econometrica* **9**, 97 – 120.

621 **Samuelson, P. A.**, 1976. Economics. 10th edition. McGraw-Hill Book
622   Company, New York.

623 **Smiseth, P. T., Wright, J., & Kölliker, M.**, 2008. Parent-offspring
624   conflict and co-adaptation: behavioural ecology meets quantitative
625   genetics. *Proceedings of the Royal Society of London Series B* **275**,
626   1823–1830.

627 **Smith, C. C. & Fretwell, S. D.**, 1974. Optimal balance between size
628   and number of offspring. *American Naturalist* **108**, 499–506.

629 **Smith, H. G., Källander, H., Fontell, K., & Ljungström, M.**, 1988.
630   Feeding frequency and parental division of labor in the double-brooded
631   great tit parus major effects - of manipulating brood size. *Behavioral*
632   *Ecology and Sociobiology* **22**, 447–453.

633 **Takada, T. & Kigami, J.**, 1991. The dynamic attainability of ESS in
634   evolutionary games. *Journal of Mathematical Biology* **29**, 513–529.

635 **Taylor, P. D. & Day, T.**, 2004. Stability in negotiation games and the
636   emergence of cooperation. *Proceedings of the Royal Society of London*
637   *Series B* **271**, 669–674.

638 **Trivers, R. L.**, 1974. Parent-offspring conflict. *American Zoologist* **14**,
639   249–264.

640 **Wolf, J. B. & Brodie, E. D.**, 1998. The coadaptation of parental and

641   offspring characters. *Evolution* **52**, 299–308.

642 **Wolfram Research, Inc.**, 2007. Mathematica Edition: Version 6.0.1.0.

643   Wolfram Research, Inc., Champaign, Illinois.

Table 1: Simulation results for behavioural and evolutionary stability for different parameter combinations p and q in the cost and benefit functions. 'NA' indicates parameter combinations with no evolutionary equilibrium in the parameter range of our simulation. 'YES' indicates parameter combinations with evolutionary equilibria which are also behavioural equilibria. 'yes' indicates parameter conditions with evolutionary equilibria that are also behavioural equilibria but where the difference of the two is larger than 0.001 (our grid resolution) in at least one dimension (supply or demand). 'no' indicates parameter combinations with evolutionary equilibria which are no behavioural equilibria. Begging cost increases from left to right. Provisioning benefit increases from top to bottom. The reason why we could not clearly assign some evolutionary equilibria to unique grid points in our simulation (p values of -0.15 and -0.2) is, that the sum of the deviations of the intercepts for the two functions was in these cases larger then the grid resolution, although taken separately each intercept fulfilled our matching criteria. Hence, our inability to assign these evolutionary equilibria is a result of our matching criteria for the intercepts rather than a methodological problem in the simulation of repeated interactions. Therefore, it is likely that these evolutionary equilibria represent the proper behavioural equilibria.

		Begging cost parameter p									
		-0.05	-0.1	-0.15	-0.2	-0.25	-0.3	-0.35	-0.4	-0.45	-0.5
Provisioning benefit parameter q	0.5	NA	YES	NA	NA	NA	NA	NA	NA	NA	NA
	1	NA	YES	yes	yes	YES	YES	YES	no	no	no
	1.5	NA	YES	yes	yes	YES	YES	YES	no	no	no
	2	NA	YES	yes	yes	YES	YES	YES	no	no	no
	2.5	NA	YES	yes	yes	YES	YES	YES	no	no	no
	3	NA	YES	yes	yes	YES	YES	YES	no	no	no
	3.5	NA	YES	yes	yes	YES	YES	YES	no	no	no
	4	NA	YES	yes	yes	YES	YES	YES	no	no	no
	4.5	NA	YES	yes	yes	YES	YES	YES	no	no	no

Figure 1: Dynamics of repeated interactions. By superimposing the demand function and the inverted supply function the repeated interdependent parent-offspring interaction can be graphically visualized. Starting at a demand level D_n (filled square) leads over repeated interactions to the supply level S_{n+4}. The equilibrium $(S_{eq}, D_{eq}$, solid diamond) represents the point of behavioural matching between parents and offspring over supply and demand level, respectively. a) A behaviourally stable parent-offspring interaction converges toward the equilibrium. b) An interaction that diverges away from the equilibrium is behaviourally not stable.

Figure 2: Illustration of the used supply and demand function types (behavioural reaction norms). a) Inverted linear supply functions (to superimpose with the demand function) for different slopes. b) Different slopes for linear demand functions. c) Several different inverted supply power functions (to superimpose with demand functions). d) Different demand power functions.

Figure 3: Supply (dashed) and demand (solid) functions which intersect in the grey shaded area represent behaviourally stable strategies (BSS). Function pairs with an intersection in the white area represent a behaviourally unstable strategy. a) Linear response functions. One supply function and two different demand functions. One combination leads to a BSS, the other is behaviourally not stable. The threshold level of 0.5 was derived analytically. b) Same as in a) but with power functions and threshold level according to the results of our numerical simulations. In a) and b) the inverted supply function is drawn to superimpose the two functions.