Behavioural attainability of evolutionarily stable strategies in repeated interactions

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Parent-Offspring Conflict

(Trivers 1974)

http://w3.shorecrest.org/~Lisa_Peck/MarineBio/syllabus/ch9vertebrates/reptilesandbirds/repbirdwp/barbara/feedingbabes.jpg
http://leonia.zoology.washington.edu/images/begging_baby_birds_border.jpg

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http://mtimages.cstv.com/byu/Homer-choke-bart.jpg

Parent-Offspring Conflict

Evolutionary resolution of conflict – ESS models

-'honest signalling' (Godfray 1991)
    parents control food allocation

-'scramble competition' (Parker&Macnair 1979)
    offspring control parental food allocation

Evolution of condition-dependent, conspicuous and costly offspring begging and parental response

Parent-Offspring Conflict

ESS models assume

- -single or multiple independent interactions (e.g., Maynard Smith 1982; Houston *et al.* 1988)
- -two-step exception (Johnstone 1996)
- -evolution strategies based on one-off behavioural interactions

But interactions are very dynamic (e.g., Chase 1980; Houston&Davies 1985; Godfray&Johnstone 2000)

Stability of evolutionary dynamics explored (e.g., Rodríguez-Gironés *et al.* 1998; McNamara *et al.* 1999)

Little known about effects of behavioural dynamics on evolutionary outcome

Behavioural Dynamics of Parent-Offspring Interactions

Behavioural reaction norm approach (Smiseth *et al.* 2008)

Expanded negotiation model framework (e.g., Moore *et al.* 1997; Taylor&Day 2004; Johnstone&Hinde 2006)

Expected behavioural equilibria (Hussell 1988, Kölliker 2003)

Equilibria of behavioural strategies considered in
- **-game-theoretical conflict resolution models** (Godfray 1991; Mock&Parker 1997; Parker *et al.* 2002)
- **-quantitative genetic coadaptation models** (Wolf&Brodie 1998; Kölliker *et al.* 2005)

Shapes of functions affect the stability of the equilibrium (Samuelson 1976)

Only behaviourally stable equilibria can adequately represent ESS

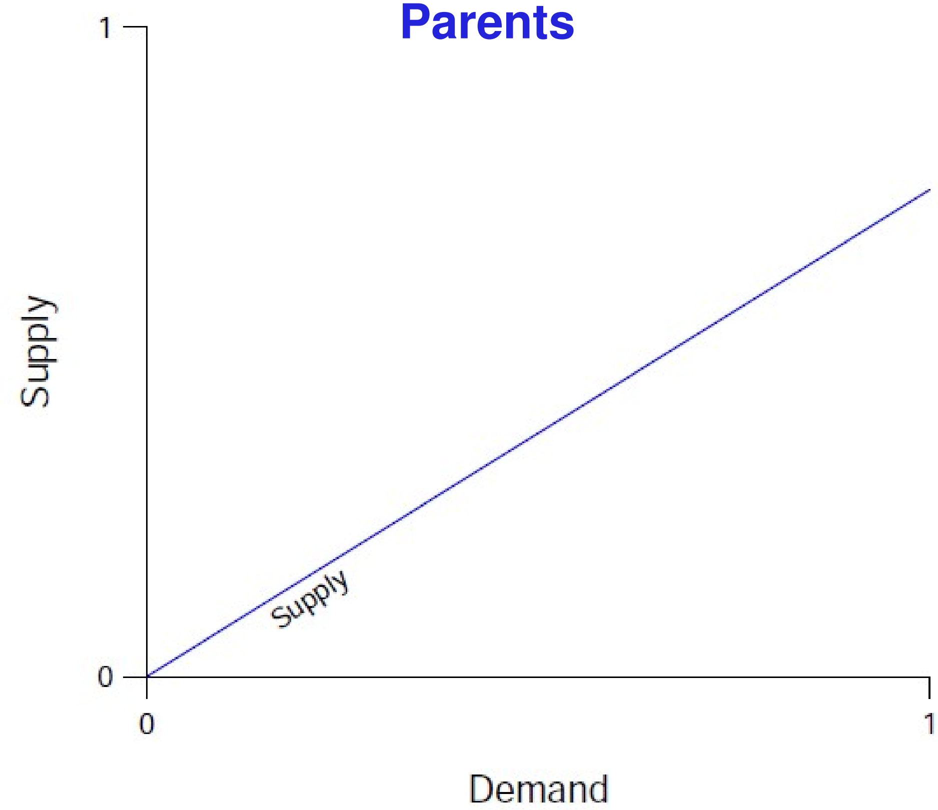
Repeated Interactions

Behavioural reaction norms

Offspring

$$D = f(S)$$

Parents



$$S = g(D)$$

Repeated Interactions

Behavioural reaction norms

Offspring

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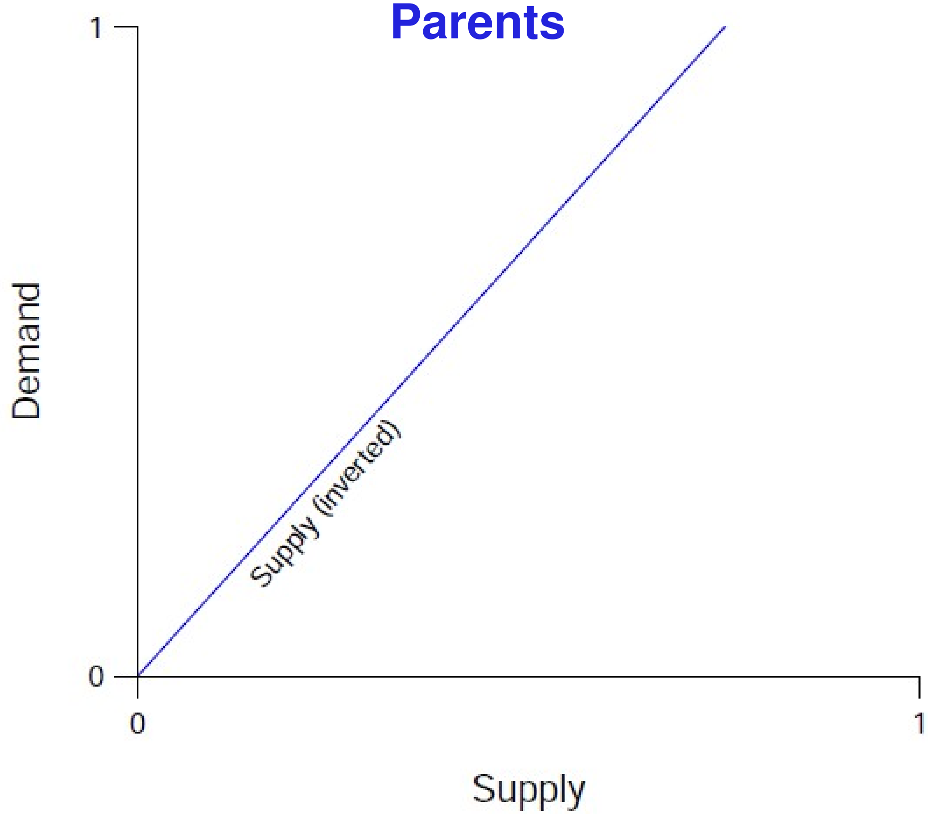
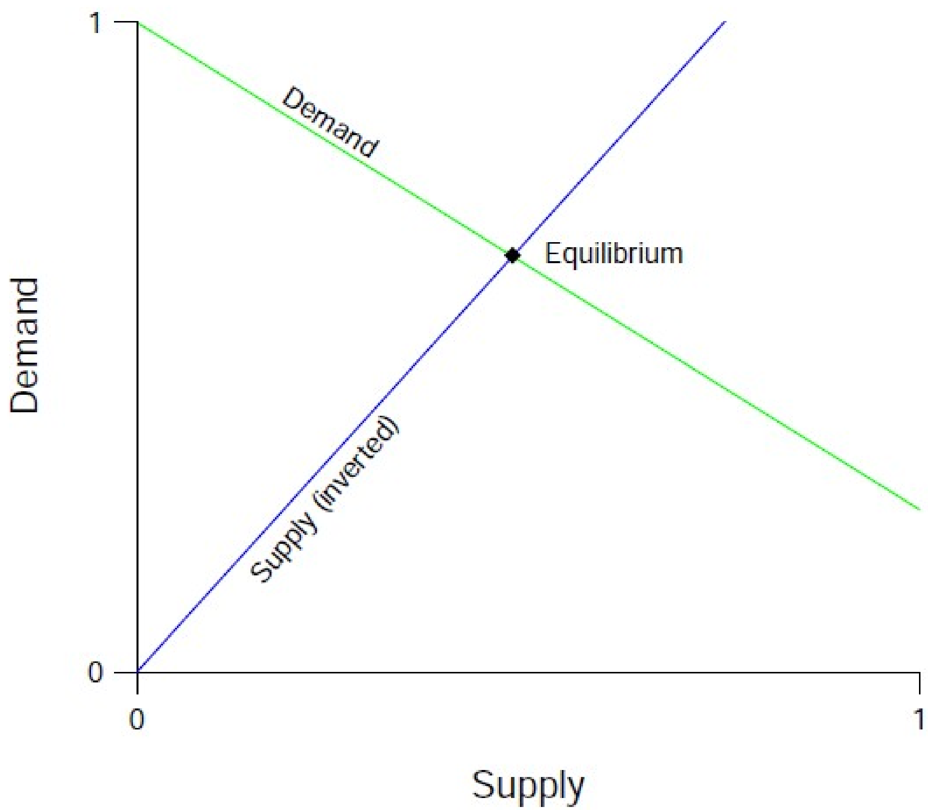


$$D = g^{-1}(S)$$

Modified after Dobler&Kölliker 2009

Behavioural Equilibrium

(Hussell 1988)



$$D = f(S) \quad Demand$$
$$D = g^{-1}(S) \quad Supply(inverted)$$

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

$$\Rightarrow S_{eq}$$

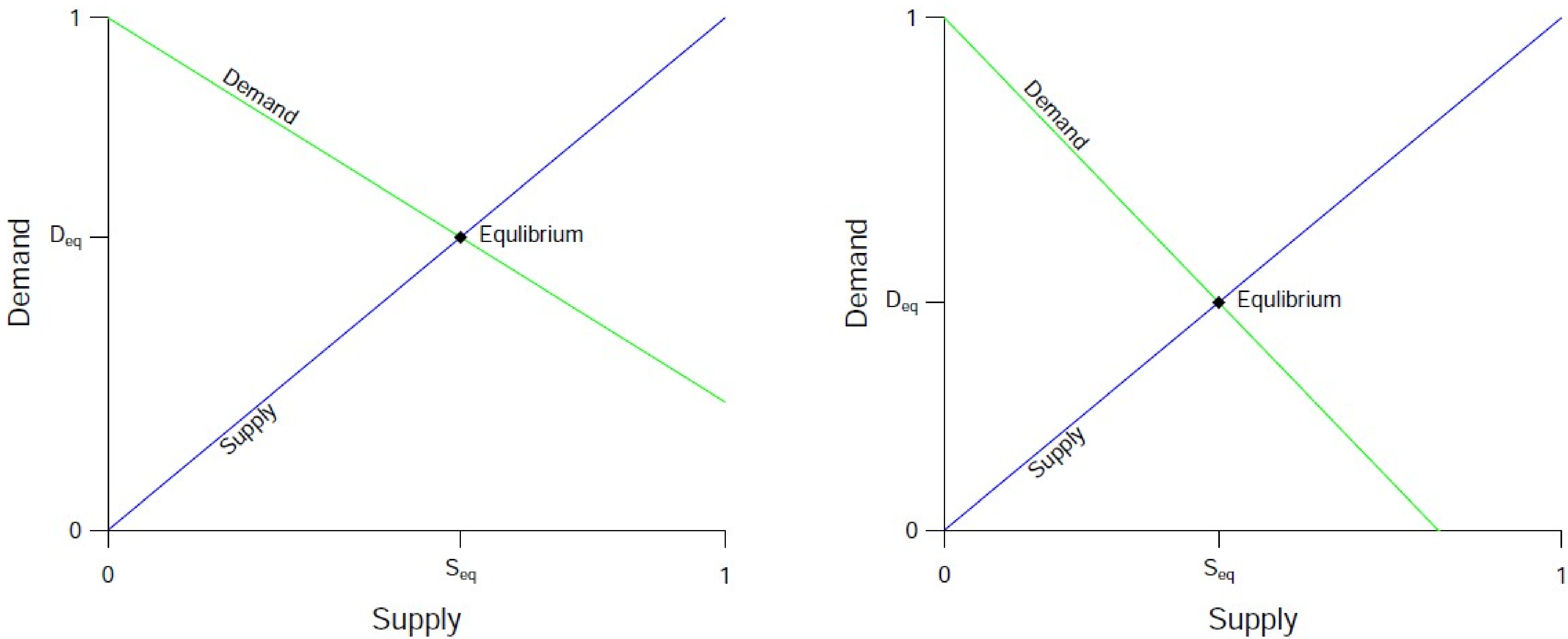
$$\Rightarrow D_{eq}$$

Repeated Interactions

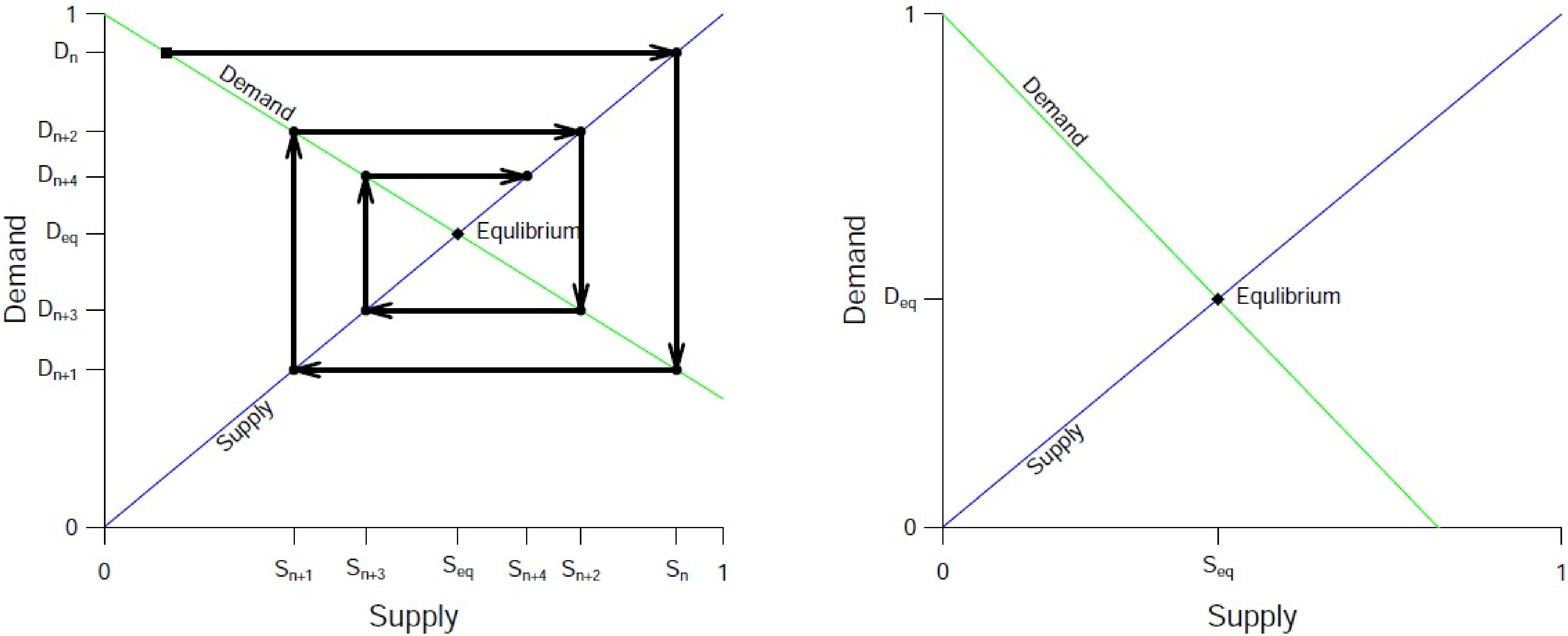
$$
\begin{aligned}
D_n &= D_n \\
S_n &= g(D_n) \\
D_{n+1} &= f(S_n) \\
S_{n+1} &= g(D_{n+1}) \\
&\vdots
\end{aligned}
$$

What are possible outcomes of repeated behavioural interactions?

Repeated Interactions

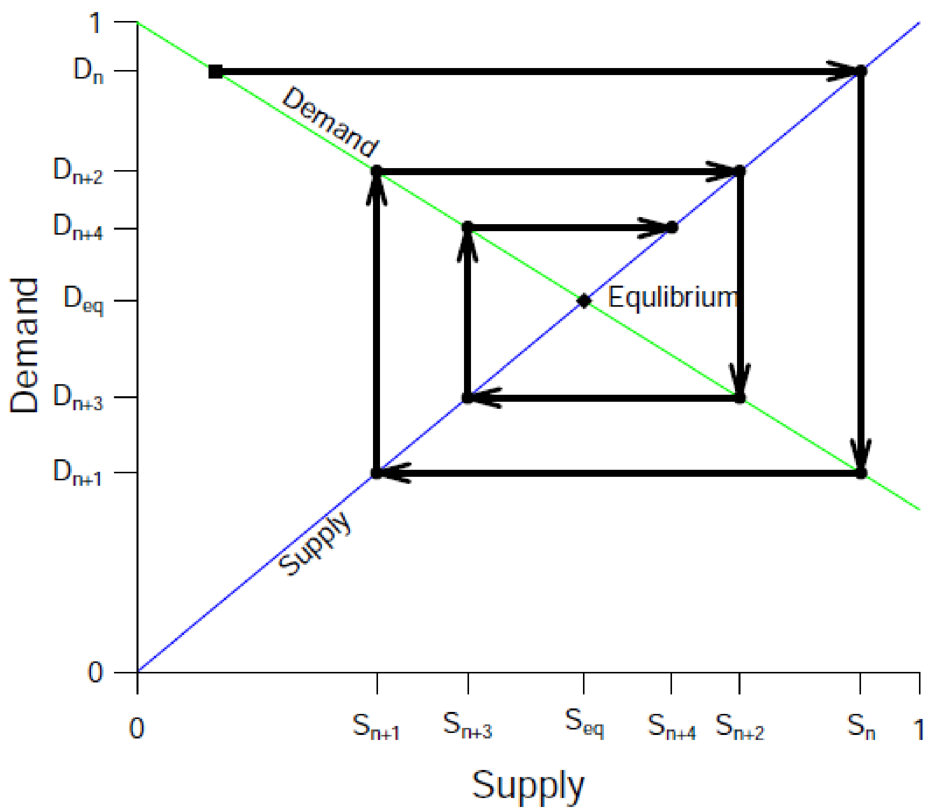


Repeated Interactions

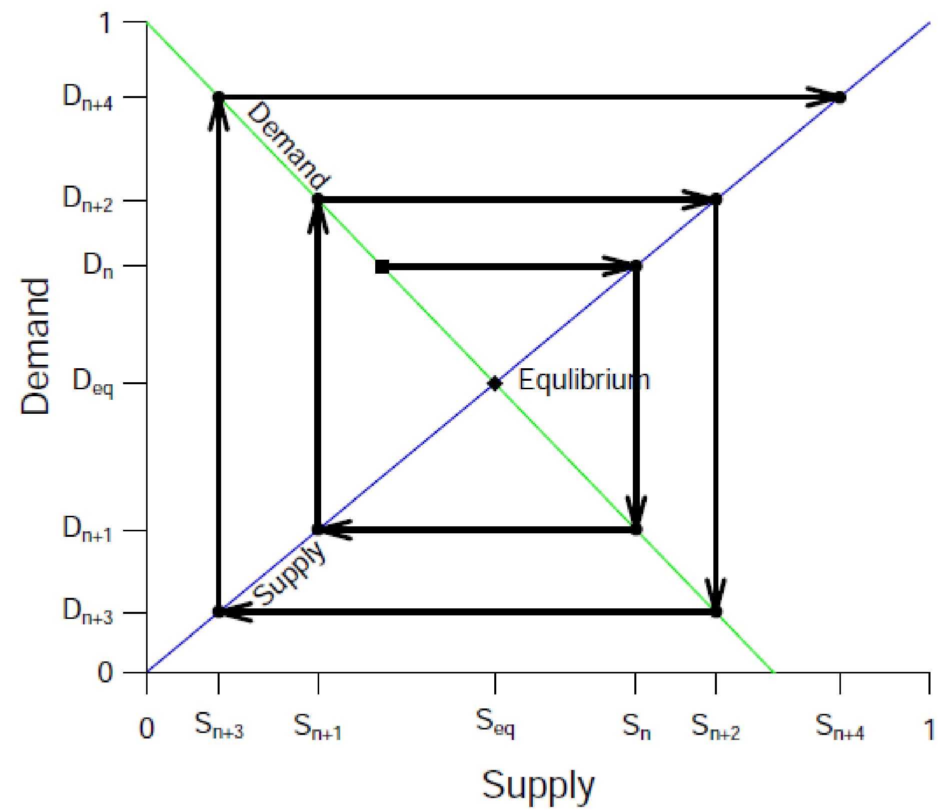


Behaviourally stable strategy (BSS)

Repeated Interactions



Behavioural stable strategy (BSS)



Behaviourally unstable strategy

When do two reaction norms represent a BSS?

Stability of Behavioural Equilibria

Discrete-time dynamics (Otto&Day 2007)

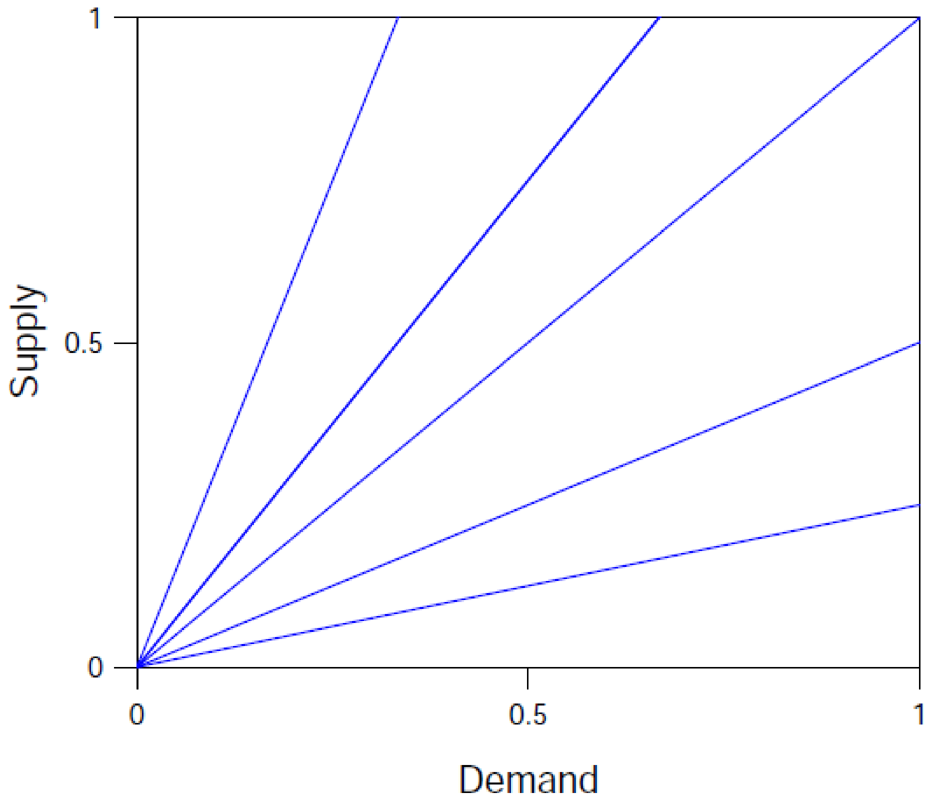
Exploring behavioural negotiation with focus on the behavioural process and allowing asymmetric functions (e.g., McNamara *et al.* 1999; Taylor&Day 2004; Johnstone&Hinde2006)

Numerical simulations

- -2000 time steps
- -supply and demand levels between 0 (minimum) and 1 (maximum)
- -strictly monotonic functions (linear and power)
- -error free parent offspring interaction
- -single parent with single offspring (Hussell 1988; Godfray 1991; Kölliker *et al.* 2005)
- -no begging means minimal provisioning
- -no provisioning means maximal begging

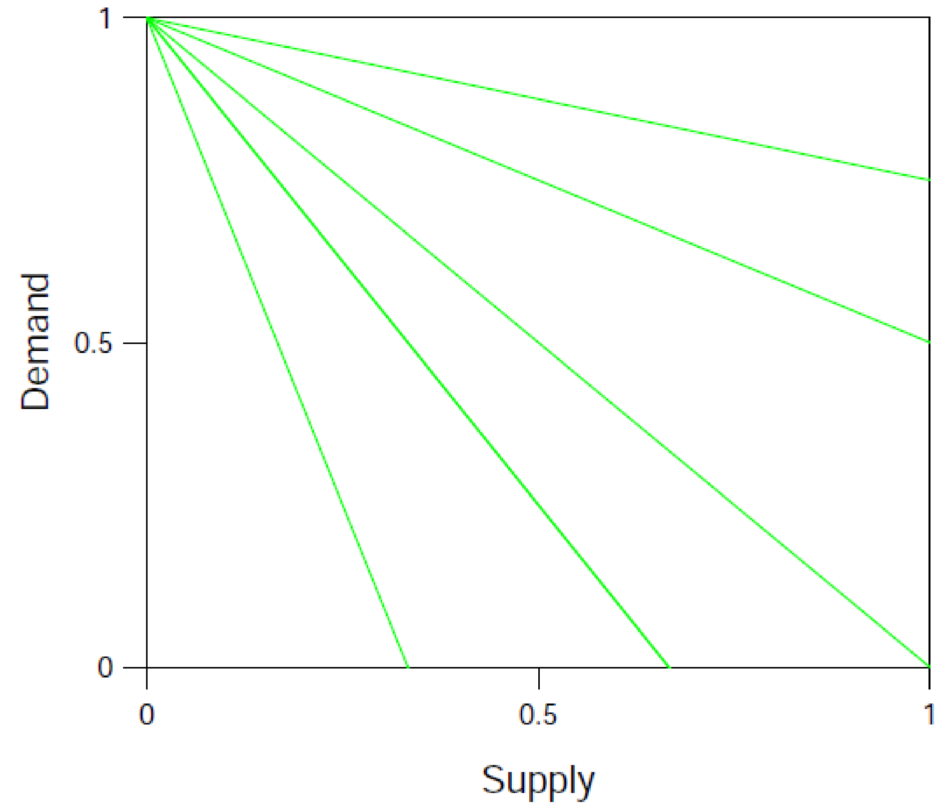
Linear Functions

Parents



$$S = g(D) = aD + y$$
$$0 < a < \infty$$
$$y = 0$$

Offspring

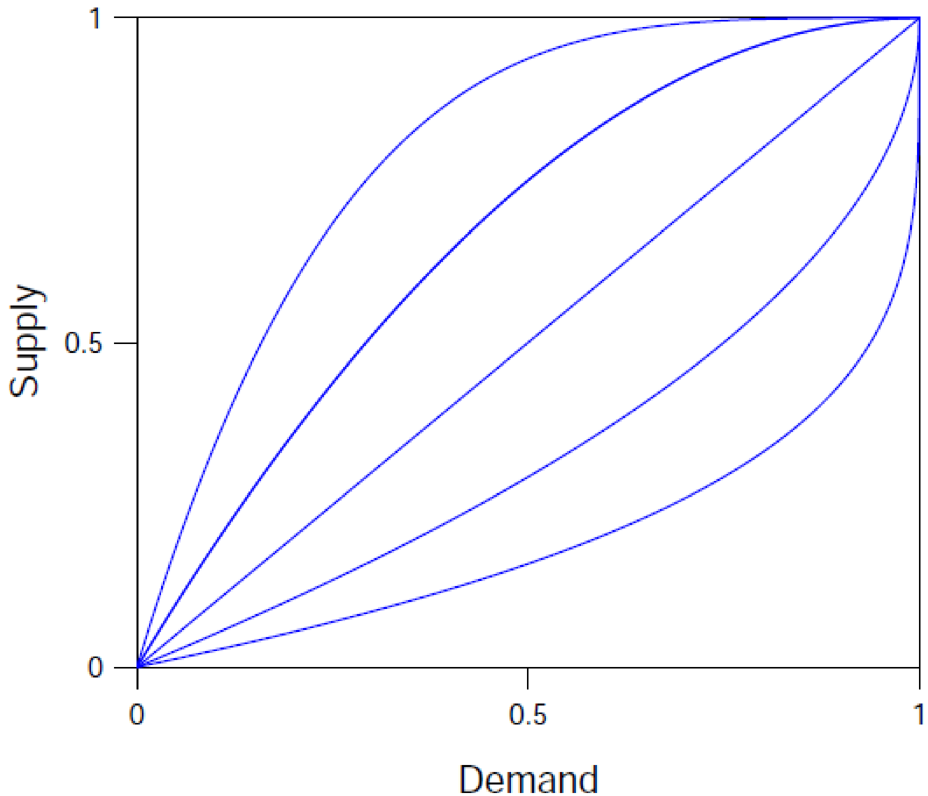


$$D = f(S) = bS + x$$
$$-\infty < b < 0$$
$$x = 1$$

Modified after Dobler&Kölliker 2009

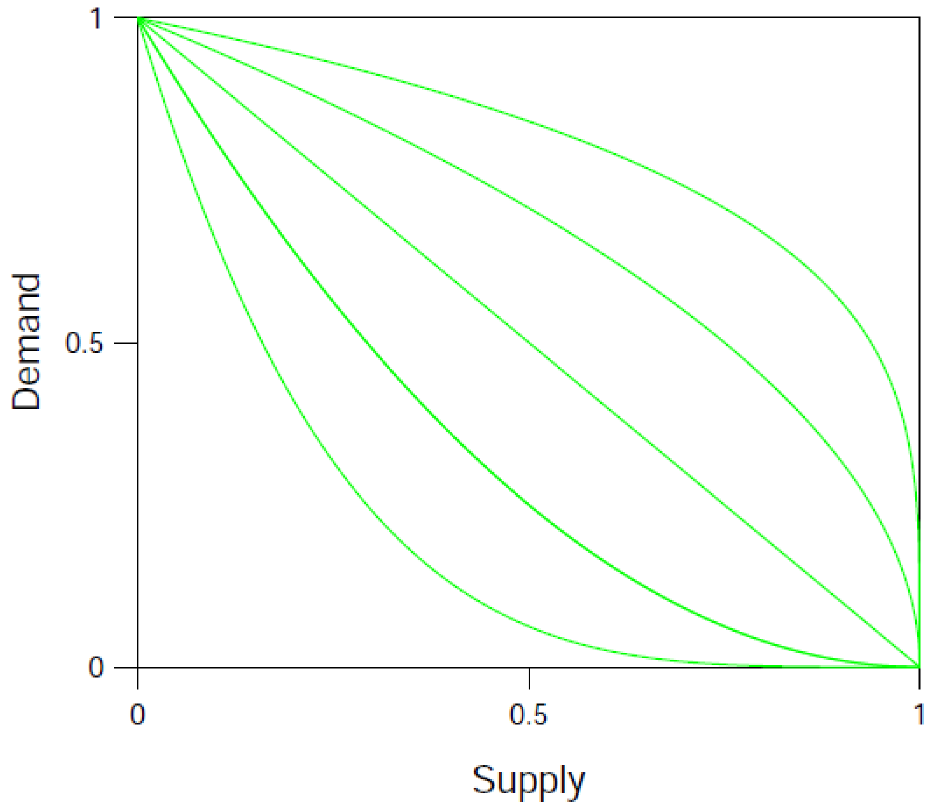
Power Functions

Parents



$$S = g(D) = 1-(1-D)^k$$
$$0 < k < \infty$$

Offspring



$$D = f(S) = (1-S)^l$$
$$0 < l < \infty$$

Stability of Behavioural Equilibria

Stability index λ (Otto&Day 2007)

$$
\begin{aligned}
\lambda = f'(S_n) = f'(g(D_n))g'(D_n) &= f'(S_n)g'(D_n) \\
f(S_n) = D_{n+1} &= b(aD_n+y)+x \\
\lambda &= ab
\end{aligned}
$$

Stability conditions for linear functions (Otto&Day 2007)

$$\lambda = |ab| < 1$$

Simulations with only positive a and negative b (Dobler&Kölliker 2009)

$$-1 < ab < 0$$

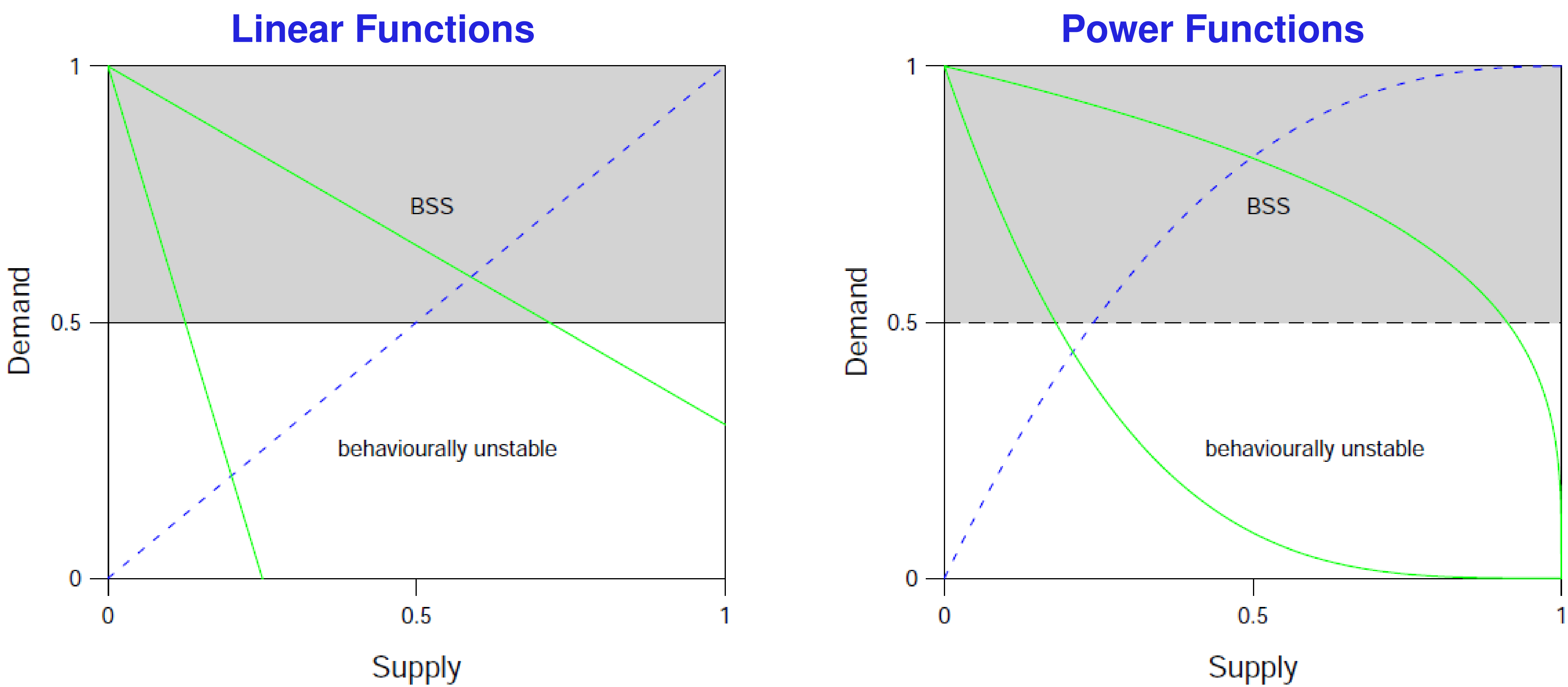
Local stability conditions for power functions (Otto&Day 2007; Dobler&Kölliker 2009)

$$-1 < f'(S_{eq})g'(D_{eq}) < 1$$

General stability conditions for power functions (Dobler&Kölliker 2009)

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

Stability of Behavioural Equilibria



$$D_{eq} > 0.5 \Rightarrow BSS$$
$$D_{eq} < 0.5 \Rightarrow \textit{not attainable}$$

Are ESS behaviourally attainable and stable?

Behavioural Attainability of ESS

Applying BSS conditions on 'scramble competition' ESS model (e.g., Mock&Parker 1997)

$$D_{ESS} = \beta \frac{\kappa(D_{ESS})}{\kappa'(D_{ESS})} = \left(\frac{0.5\,ab}{ab-1}\right)\frac{p\,D_{ESS}+1}{D_{ESS}}; \quad p = begging\,cost\,parameter$$

$$S_{ESS} = \alpha \frac{\mu(S_{ESS})}{\mu'(S_{ESS})} = \left(1-\frac{0.5\,ab}{ab-1}\right)\frac{1-e^{-q(S_{ESS}-0.1)}}{e^{-q(S_{ESS}-0.1)}k}; \quad q = provisioning\,benefit\,parameter$$

Numerical sensitivity analysis with 90 p-q-combinations on 1'000'000 slope combinations

- -calculate ESS
- -control intercepts
- -ESS at same grid point like slope intersection (equilibrium)
- -one expected ESS for each p-q-combination
- -equilibrium behaviourally stable/attainable

Behavioural Attainability of ESS

Provisioning benefit parameter q	Begging cost parameter p									
	-0.05	-0.1	-0.15	-0.2	-0.25	-0.3	-0.35	-0.4	-0.45	-0.5
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

Modified after Dobler&Kölliker 2009

Behaviourally Stable Strategies BSS

Slopes define the stability of the interaction

- -unstable interaction when one interactant reacts to sensitively (Samuelson 1941,1976)
- -interactions only stable for intermediate to high begging levels

Biological rationale for $|\lambda|$ in other models

- -negotiation models (McNamara *et al.* 1999; Taylor&Day 2004; Johnstone&Hinde 2006)
- -quantitative genetic models (Moore *et al.* 1997; Kölliker 2003)

Behaviourally Stable Strategies BSS

Incorporate more realism

- -communication errors
- -time lags
- -function adjustments (Johnstone&Grafen 1992; Johnstone 1994)
- -three-way interactions
  - mother with two offspring
  - two parents with one offspring

Complexer functions with multiple equilibria

- -stable and unstable equilibria possible?
- -how to change from one equilibrium to another?

Behaviourally Stable Strategies BSS

Apply to experimental work

- **-average effects investigated** (e.g., Smith *et al.* 1988; Kilner 1995; Ottosson *et al.* 1997; Kilner *at al.* 1999)
- **-BSS should stabilise back after disturbance**

Applies also for other fast-responding short-term interactions

- **-cell interactions** (Hofmeyr&Cornish-Bowden 2000)
- **-biological markets** (Noe&Hammerstein 1994;1995)
- **-negotiation over care** (e.g., McNamara *et al.* 1999; Taylor&Day 2004; Johnstone&Hinde2006)

Behavioural Attainability of ESS

ESS predicted by the 'scramble competition' resolution model

- -behaviourally stable
- -outside the parameter range
- -behaviourally unstable and hence not attainable

Intermediate to high begging levels are favoured by selection

- -at low to intermediate begging costs

Take Home Message

Dynamic behavioural interactions have strong effects on the evolutionary outcome of parent-offspring conflicts

BSS and ESS conditions have to be met for evolutionary stability in a stricter sense

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