

## Prey-predator coevolution

### New features

- coevolutionary dynamics of different species
- coevolutionary cycles
- different kinds of stability
- predator induced branching in the prey

### Strategy

$x, y$  are, respectively, prey and predator log-body mass.

### Full population dynamics

$$\frac{d}{dt} m_i = r[x_i] m_i \left( 1 - \frac{\sum_{j=1}^k a[x_i, x_j] m_j}{K[x_i]} \right) - m_i \sum_{j=1}^l b[x_i, y_j] n_j \quad (i = 1, \dots, k) \quad (\text{prey})$$

$$\frac{d}{dt} n_i = n_i \sum_{j=1}^k c[x_j, y_i] b[x_j, y_i] m_j - d[y_i] n_i \quad (i = 1, \dots, l) \quad (\text{predator})$$

### MONOMORPHIC PREY POPULATION and MONOMORPHIC PREDATOR POPULATION

#### Population equations

$m$  = prey pop dens;  $n$  = pred pop dens;  $x$  = prey log body size;  $y$  = pred log body size

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$$d\text{Logm}[m, n] := r[x] \left( 1 - \frac{a[x, x] m}{k[x]} \right) - b[x, y] n;$$

$$d\text{Logn}[m, n] := c[x, y] b[x, y] m - d[y];$$


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#### Population equilibrium

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$$\text{Solve}[\{d\text{Logm}[m, n] == 0, d\text{Logn}[m, n] == 0\}, \{m, n\}]$$


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$$\left\{ \left\{ n \rightarrow \frac{r[x]}{b[x, y]} - \frac{a[x, x] d[y] r[x]}{b[x, y]^2 c[x, y] k[x]}, m \rightarrow \frac{d[y]}{b[x, y] c[x, y]} \right\} \right\}$$


---

$$m[\{x, y\}] := \frac{d[y]}{b[x, y] c[x, y]};$$

$$n[\{x, y\}] := \frac{r[x]}{b[x, y]} - \frac{a[x, x] d[y] r[x]}{b[x, y]^2 c[x, y] k[x]};$$


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## Parameter values and functions

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```

r[x_] := 1;

k[x_] := e-x2;

a[x1_, x2_] := e-α(x1-x2)2; α = 0.5;

b[x_, y_] := β1 e-β2(x-y-p)2; β1 = 100; β2 = 0.2; p = Log[0.5];

c[x_, y_] := γ ex-y; γ = 0.2;

d[y_] := δ1 e-δ2 y; δ1 = 1; δ2 = 1;

```

---

## Coexistence

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```

xmin = -1.5; xmax = 2.5; ymin = -3.5; ymax = 6;

```

---

```

coexBnd = ContourPlot[If[m[{x, y}] > 0 && n[{x, y}] > 0, 1, -1],
  {x, xmin, xmax}, {y, ymin, ymax}, Contours → {0}, ContourStyle → {Black},
  ContourShading → False, PlotPoints → 60];

```

---

```

preyInt = DensityPlot[If[m[{x, y}] > 0 && n[{x, y}] > 0, m[{x, y}], k[x]],
  {x, xmin, xmax}, {y, ymin, ymax}, ColorFunction → "AvocadoColors",
  PlotPoints → 60];

```

---

```

predInt = DensityPlot[If[m[{x, y}] > 0 && n[{x, y}] > 0, n[{x, y}]],
  {x, xmin, xmax}, {y, ymin, ymax}, ColorFunction → "SolarColors",
  PlotPoints → 60];

```

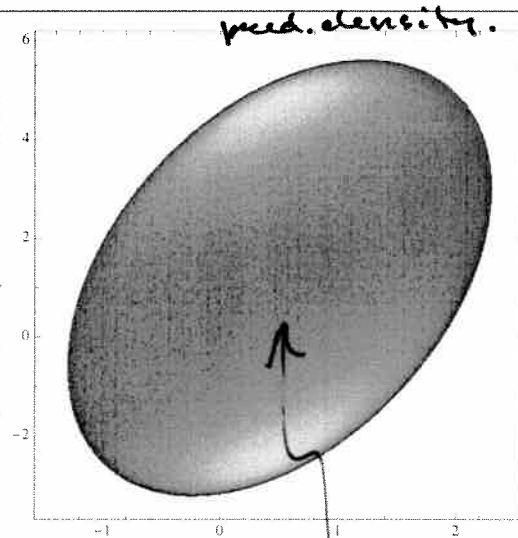
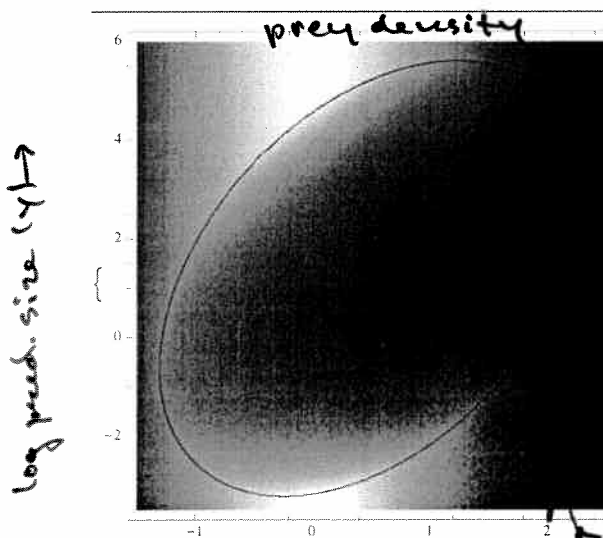
---

```

{Show[preyInt, coexBnd], Show[predInt, coexBnd]}

```

---



log prey size (x) →

prey can also exist without predator.

pred. can only exist for (x,y) combinations in here

## Invasion fitness

Prey invasion fitness and its derivatives

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```

sPreymo[{x_, y_}, X_] := r[X] (1 - a[X, x] m[{x, y}] / k[X]) - b[X, y] n[{x, y}];

dsPreymo[{x_, y_}] :=  $\partial_x$  sPreymo[{x, y}, X] /. {X → x};

ddsPreymo[{x_, y_}] :=  $\partial_{x,x}$  sPreymo[{x, y}, X] /. {X → x};

```

---

Predator invasion fitness and its derivatives:

---

```

sPredmo[{x_, y_}, Y_] := c[x, Y] b[x, Y] m[{x, y}] - d[Y];

dsPredmo[{x_, y_}] :=  $\partial_Y$  sPredmo[{x, y}, Y] /. {Y → y};

ddsPredmo[{x_, y_}] :=  $\partial_{Y,Y}$  sPredmo[{x, y}, Y] /. {Y → y};

```

---

## Isocline plot

Prey isoclines

*solid = evolutionarily stable; dashed = not evolutionarily stable*

---

```

preyES = ContourPlot[If[n[{x, y}] > 0 && ddsPreymo[{x, y}] ≤ 0,
  dsPreymo[{x, y}]], {x, xmin, xmax}, {y, ymin, ymax}, Contours → {0},
  ContourShading → False, ContourStyle → {Black, Thick}, PlotPoints → 30];

preyNES = ContourPlot[If[n[{x, y}] > 0 && ddsPreymo[{x, y}] > 0,
  dsPreymo[{x, y}]], {x, xmin, xmax}, {y, ymin, ymax}, Contours → {0},
  ContourShading → False, ContourStyle → {Black, Thick, Dashed},
  PlotPoints → 30];

```

---

Predator isoclines

*solid = evolutionarily stable; dashed = not evolutionarily stable*

---

```

predES = ContourPlot[If[n[{x, y}] > 0 && ddsPredmo[{x, y}] ≤ 0,
  dsPredmo[{x, y}]], {x, xmin, xmax}, {y, ymin, ymax}, Contours → {0},
  ContourShading → False, ContourStyle → {Red, Thick}, PlotPoints → 30];

predNES = ContourPlot[If[n[{x, y}] > 0 && ddsPredmo[{x, y}] > 0,
  dsPredmo[{x, y}]], {x, xmin, xmax}, {y, ymin, ymax}, Contours → {0},
  ContourShading → False, ContourStyle → {Red, Thick, Dashed},
  PlotPoints → 30];

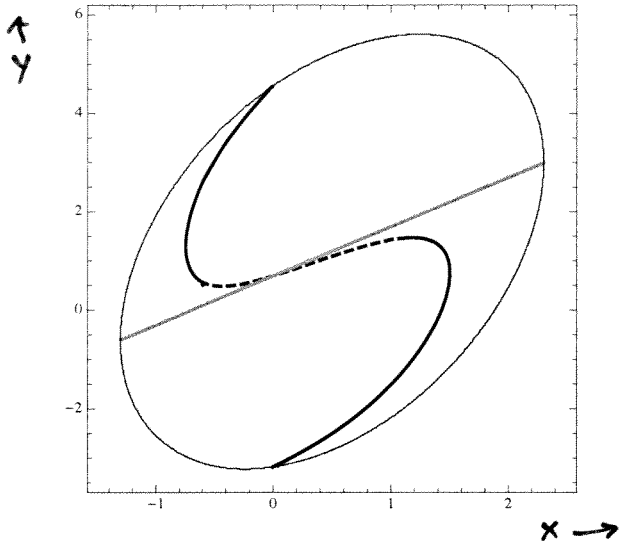
```

---

## Isocline plot

(black = prey isocline; red = predator isocline; solid = ES; dashed = NES)

Show[preyES, preyNES, predES, predNES, coexBnd]



## Canonical equation

Mutation rate and standard deviation of the mutant step distribution; only the relative prey/pred sizes matter

$$\mu_{\text{Prey}} = 1;$$

$$\sigma_{\text{Prey}} = 1;$$

$$\mu_{\text{Pred}} = 1;$$

$$\sigma_{\text{Pred}} = 1;$$

## Deterministic drift

$$\text{drift}_{\text{mo}}[\{x_, y_}] :=$$

$$\left\{ \frac{1}{2} \mu_{\text{Prey}} \sigma_{\text{Prey}}^2 m[\{x, y\}] \text{dsPrey}_{\text{mo}}[\{x, y\}], \right. \\ \left. \frac{1}{2} \mu_{\text{Pred}} \sigma_{\text{Pred}}^2 n[\{x, y\}] \text{dsPred}_{\text{mo}}[\{x, y\}] \right\};$$

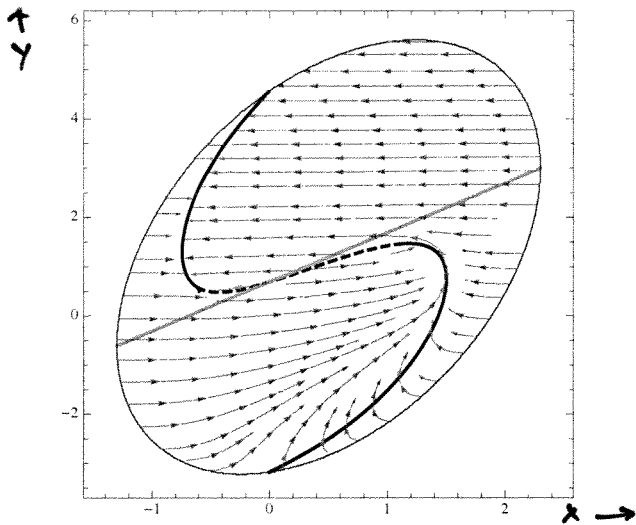
## Stream plot (CE)

---

```
CEstream = StreamPlot[If[n[{x, y}] > 0, driftmo[{x, y}], {0, 0}],
  {x, xmin, xmax}, {y, ymin, ymax}];
```

```
Show[preyES, preyNES, predES, predNES, coexBnd, CEstream]
```

---



## Deterministic orbit (Euler method)

---

```
v0 = {-1, -2}; (* starting point of orbit *)
t0 = 0; (* start time *)
t∞ = 20000; (* stop time *)
Δt = 1; (* integration time step *)

data = {};
v = v0;
t = t0;
While[t ≤ t∞ && n[v] > 0,
  data = Join[data, {Append[v, t]}];
  v = v + Δt driftmo[v];
  t = t + Δt;
];
```

---

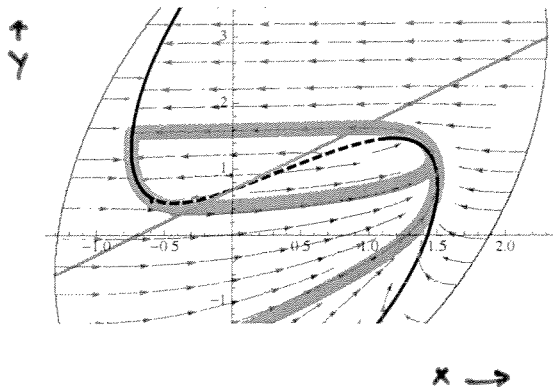
## Projected orbit on the (x,y)-plane

---

```
CEorbit = ListPlot[data[[All, {1, 2}]], PlotStyle → {Gray, PointSize[0.03]},
  Joined → False];
```

```
Show[CEorbit, preyES, preyNES, predES, predNES, coexBnd, CEstream]
```

---



*evolutionary  
cycle.*

## Orbit as evolutionary tree

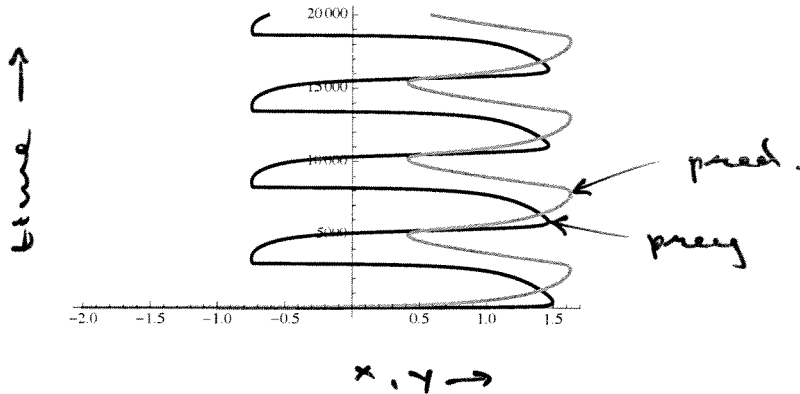
---

```

xtree = ListPlot[data[[All, {1, 3}]], PlotStyle -> {Black, Thick},
  Joined -> True];
ytree = ListPlot[data[[All, {2, 3}]], PlotStyle -> {Red, Thick},
  Joined -> True];
Show[xtree, ytree]

```

---



## Stability

Jacobi matrix for stability calculations

---

```

Jxx[{x_, y_}] := (D[x1, x2] sPrey_mo[{X1, y}, X2] + D[x2, x2] sPrey_mo[{x, y}, X2]) /.
  {X1 -> x, X2 -> x};

Jxy[{x_, y_}] := D[x, y] sPrey_mo[{x, Y}, X] /. {X -> x, Y -> y};

Jyx[{x_, y_}] := D[x, y] sPred_mo[{X, Y}, Y] /. {X -> x, Y -> y};

Jyy[{x_, y_}] := (D[y1, y2] sPred_mo[{x, Y1}, Y2] + D[y2, y2] sPred_mo[{x, y}, Y2]) /.
  {Y1 -> y, Y2 -> y};

```

---

Total stability

---

```

totStab =
  DensityPlot[
    If[n[{x, y}] > 0 && Jxx[{x, y}] < 0 && Jyy[{x, y}] < 0 &&
      Jxx[{x, y}] Jyy[{x, y}] > Abs[Jxy[{x, y}] Jyx[{x, y}]],
      Abs[dsPrey_mo[{x, y}]] + Abs[dsPred_mo[{x, y}]]], {x, xmin, xmax},
    {y, ymin, ymax}, ColorFunction -> "FuchsiaTones", PlotPoints -> 60];

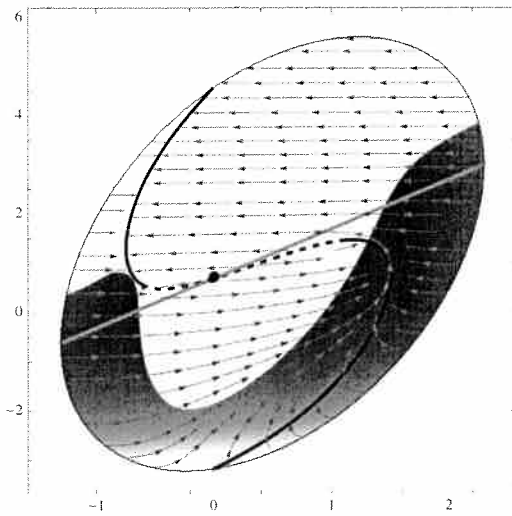
```

---

---

```
Show[totStab, preyES, preyNES, predES, predNES, CEstream, coexBnd]
```

---



*Conclusion: the intersection of the isoclines is NOT ABSOLUTELY STABLE.*

Strong stability

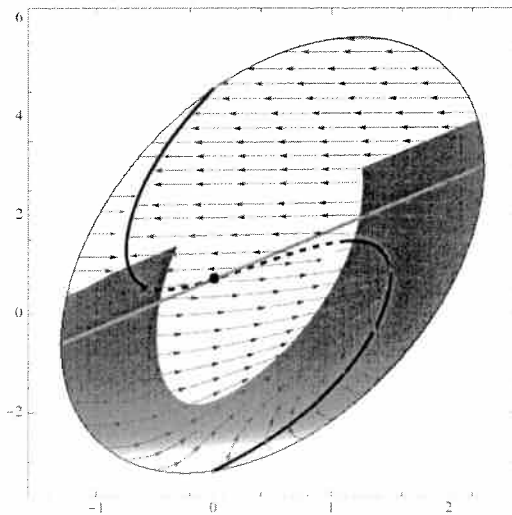
---

```
strStab =
  DensityPlot[
    If[n[{x, y}] > 0 && Jxx[{x, y}] < 0 && Jyy[{x, y}] < 0 &&
      Jxx[{x, y}] Jyy[{x, y}] > Jxy[{x, y}] Jyx[{x, y}],
      Abs[dsPreymo[{x, y}]] + Abs[dsPredmo[{x, y}]]], {x, xmin, xmax},
    {y, ymin, ymax}, ColorFunction -> "CherryTones", PlotPoints -> 60];
```

---

```
Show[strStab, preyES, preyNES, predES, predNES, CEstream, coexBnd]
```

---



*Conclusion: the intersection of the isoclines is NOT STRONGLY STABLE.*

## Weak stability

---

```

wkStab =
  DensityPlot[
    If[n[{x, y}] > 0 &&
       $\mu_{\text{Prey}} \sigma_{\text{Prey}}^2 m[\{x, y\}] J_{xx}[\{x, y\}] + \mu_{\text{Pred}} \sigma_{\text{Pred}}^2 n[\{x, y\}] J_{yy}[\{x, y\}] <$ 
      0 &&  $J_{xx}[\{x, y\}] J_{yy}[\{x, y\}] > J_{xy}[\{x, y\}] J_{yx}[\{x, y\}]$ ,
      Abs[dsPreymo[\{x, y\}]] + Abs[dsPredmo[\{x, y\}]]], {x, xmin, xmax},
    {y, ymin, ymax}, ColorFunction → "CoffeeTones", PlotPoints → 60];

```

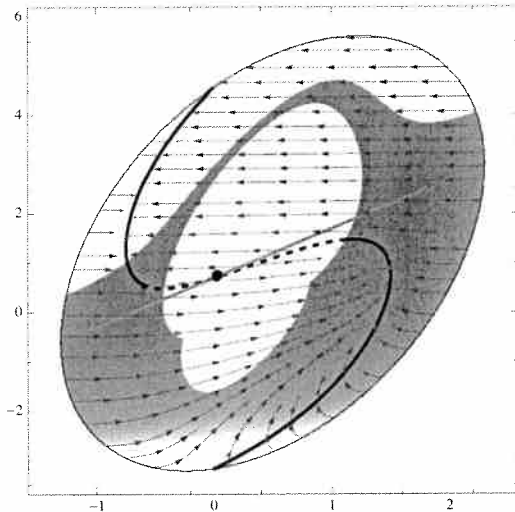
---

```

Show[wkStab, preyES, preyNES, predES, predNES, CEstream, coexBnd]

```

---



Conclusion: the intersection of the isoclines is for the present mutation rates and mutation variances **NOT WEAKLY STABLE**

The relative mutation rates and/or mutation standard deviations can affect weak stability, but not absolute and strong stability.

---

```

 $\mu_{\text{Prey}} = 1;$ 
 $\sigma_{\text{Prey}} = 0.1;$ 
 $\mu_{\text{Pred}} = 1;$ 
 $\sigma_{\text{Pred}} = 1;$ 

```

---

```

wkStab =
  DensityPlot[
    If[n[{x, y}] > 0 &&
       $\mu_{\text{Prey}} \sigma_{\text{Prey}}^2 m[\{x, y\}] J_{xx}[\{x, y\}] + \mu_{\text{Pred}} \sigma_{\text{Pred}}^2 n[\{x, y\}] J_{yy}[\{x, y\}] <$ 
      0 &&  $J_{xx}[\{x, y\}] J_{yy}[\{x, y\}] > J_{xy}[\{x, y\}] J_{yx}[\{x, y\}]$ ,
      Abs[dsPreymo[\{x, y\}]] + Abs[dsPredmo[\{x, y\}]]], {x, xmin, xmax},
    {y, ymin, ymax}, ColorFunction → "CoffeeTones", PlotPoints → 60];

```

---

```

CEstream = StreamPlot[If[n[{x, y}] > 0, driftmo[\{x, y\}], {0, 0}],
  {x, xmin, xmax}, {y, ymin, ymax}];

```

---

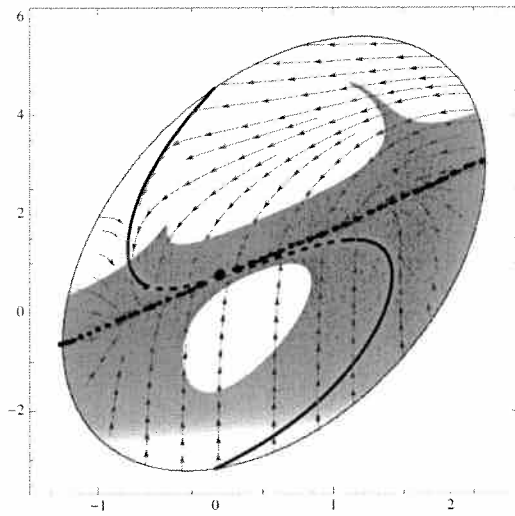


## Weak stability for the new mutation parameter values

---

```
Show[wkStab, preyES, preyNES, predES, predNES, CEstream, coexBnd]
```

---



Conclusion: for the new mutation rates and mutation variances, the intersection of the isoclines is WEAKLY STABLE.

## Deterministic orbit (CE)

---

```
v0 = {1.5, 4.5}; (* starting point of orbit *)
t0 = 0; (* start time *)
t∞ = 200000; (* stop time *)
Δt = 50; (* integration time step *)

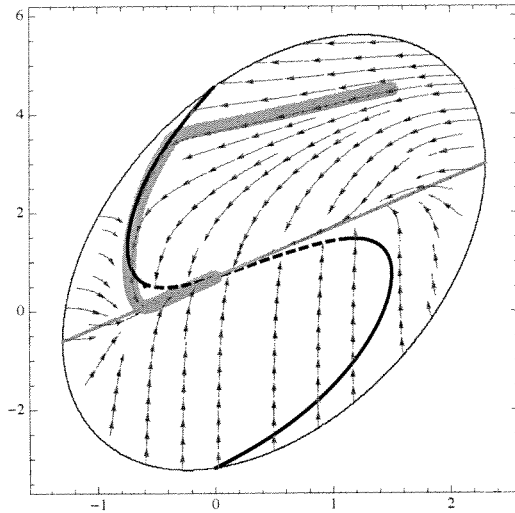
data = {};
v = v0;
t = t0;
While[t ≤ t∞ && n[v] > 0,
  data = Join[data, {Append[v, t]}];
  v = v + Δt driftmo[v];
  t = t + Δt;
];
```

---

Projected orbit on the (x,y)-plane

```
CEorbit = ListPlot[data[[All, {1, 2}]], PlotStyle -> {Gray, PointSize[0.03]},
  Joined -> False];
```

```
Show[coexBnd, CEorbit, preyES, preyNES, predES, predNES, CEstream]
```



### Evolutionary branching in the prey?

Notice that the prey-isocline near the intersection is not evolutionarily stable (dashed isocline). Does that mean that the prey strategy will branch?

Pairwise invadability plot (PIP) for the prey in the neighborhood of the intersection of the prey-predator isoclines

```
PIPbnd = ContourPlot[If[n[{x, 0.69}] > 0, sPrey_mo[{x, 0.69}, X]],
  {x, xmin, xmax}, {X, xmin, xmax}, Contours -> {0},
  ContourStyle -> {Black, Thick}, ContourShading -> False, PlotPoints -> 60];
```

```
nPos = ContourPlot[n[{x, 0.69}], {x, xmin, xmax}, {X, xmin, xmax},
  Contours -> {0}, ContourStyle -> {Black, Thick}, ContourShading -> False,
  PlotPoints -> 60];
```

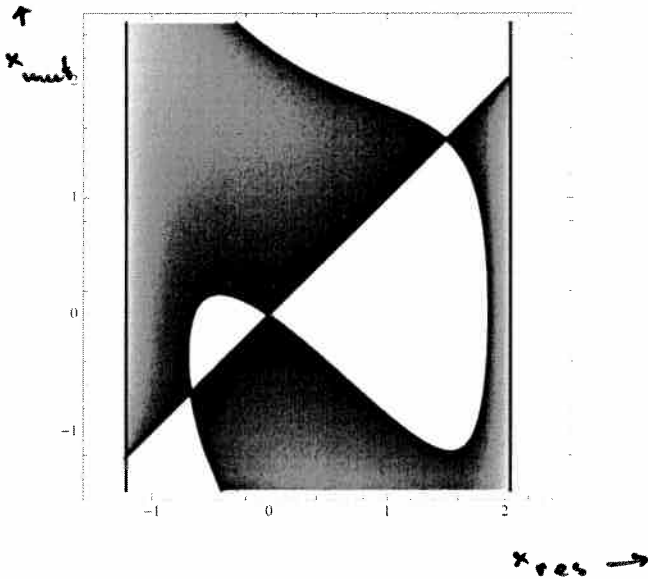
```
PIPint = DensityPlot[If[n[{x, 0.69}] > 0 && sPrey_mo[{x, 0.69}, X] > 0,
  sPrey_mo[{x, 0.69}, X]], {x, xmin, xmax}, {X, xmin, xmax},
  ColorFunction -> "AvocadoColors", PlotPoints -> 60];
```

Pairwise invadability plot (PIP) for fixed predator trait

---

Show[PIPint, PIPbnd, nPos]

---



Mutual invadability plot (MIP) for the prey in the neighborhood of the intersection of the prey-predator isoclines (detail)

---

MIPbnd =

```
ContourPlot[If[Abs[x - X] > 0.001,
  sPrey_mo[{x, 0.69}, X] sPrey_mo[{X, 0.69}, x]], {x, -0.5, 0.5},
  {X, -0.5, 0.5}, Contours -> {0}, ContourStyle -> {Black, Thick},
  ContourShading -> False, PlotPoints -> 60];
```

```
MIPint = DensityPlot[If[sPrey_mo[{x, 0.69}, X] > 0 && sPrey_mo[{X, 0.69}, x] > 0,
  sPrey_mo[{x, 0.69}, X] sPrey_mo[{X, 0.69}, x]], {x, -0.5, 0.5},
  {X, -0.5, 0.5}, ColorFunction -> "AvocadoColors", PlotPoints -> 60];
```

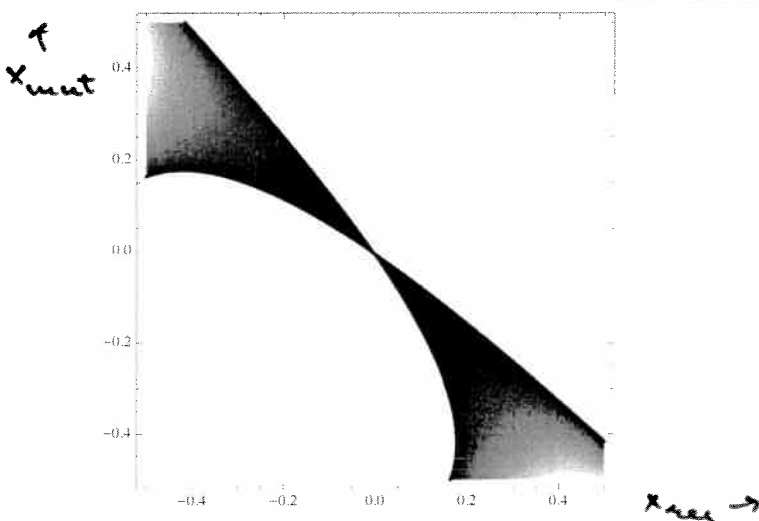
---

Mutual invadability plot (MIP) for fixed predator trait

---

Show[MIPint, MIPbnd]

---



Conclusion: evolutionary branching cannot yet be excluded. Since the cone of mutual invadability is so very narrow, the dimorphic prey orbit might not stay inside it. This we have to investigate further . . .

## DIMORPHIC PREY POPULATION and MONOMORPHIC PREDATOR POPULATION

Reset

---

```
Clear[r, k, a, b, c, d];
```

---

Population equations

$m_1, m_2$  = prey pop dens;  $nn$  = pred pop dens;  $x_1, x_2$  = prey log body size;  $y$  = pred log body size

---


$$dLogm1[m1_, m2_, nn_] := r[x1] \left( 1 - \frac{a[x1, x1] m1 + a[x1, x2] m2}{k[x1]} \right) - b[x1, y] nn;$$

$$dLogm2[m1_, m2_, nn_] := r[x2] \left( 1 - \frac{a[x2, x1] m1 + a[x2, x2] m2}{k[x2]} \right) - b[x2, y] nn;$$

$$dLognn[m1_, m2_, nn_] := c[x1, y] b[x1, y] m1 + c[x2, y] b[x2, y] m2 - d[y];$$


---

Population equilibrium

---

```
Solve[{dLogm1[m1, m2, nn] == 0, dLogm2[m1, m2, nn] == 0,
      dLognn[m1, m2, nn] == 0}, {m1, m2, nn}]
```

---

$$\left\{ \left\{ nn \rightarrow - \left( -a[x1, x2] a[x2, x1] d[y] r[x1] r[x2] + a[x1, x1] a[x2, x2] d[y] r[x1] r[x2] - \right. \right. \right.$$

$$\left. \left. \begin{aligned} & a[x2, x2] b[x1, y] c[x1, y] k[x1] r[x1] r[x2] + a[x2, x1] b[x2, y] c[x2, y] k[x1] r[x1] r[x2] + \\ & a[x1, x2] b[x1, y] c[x1, y] k[x2] r[x1] r[x2] - a[x1, x1] b[x2, y] c[x2, y] k[x2] r[x1] r[x2] \end{aligned} \right) / \right.$$

$$\left. \left( -a[x1, x2] b[x1, y] b[x2, y] c[x1, y] k[x2] r[x1] + a[x1, x1] b[x2, y]^2 c[x2, y] k[x2] r[x1] + \right. \right.$$

$$\left. \left. a[x2, x2] b[x1, y]^2 c[x1, y] k[x1] r[x2] - a[x2, x1] b[x1, y] b[x2, y] c[x2, y] k[x1] r[x2] \right), \right.$$

$$m1 \rightarrow - \left( a[x1, x2] b[x2, y] d[y] k[x2] r[x1] - b[x2, y]^2 c[x2, y] k[x1] k[x2] r[x1] - \right.$$

$$\left. \left. a[x2, x2] b[x1, y] d[y] k[x1] r[x2] + b[x1, y] b[x2, y] c[x2, y] k[x1] k[x2] r[x2] \right) / \right.$$

$$\left. \left( -a[x1, x2] b[x1, y] b[x2, y] c[x1, y] k[x2] r[x1] + a[x1, x1] b[x2, y]^2 c[x2, y] k[x2] r[x1] + \right. \right.$$

$$\left. \left. a[x2, x2] b[x1, y]^2 c[x1, y] k[x1] r[x2] - a[x2, x1] b[x1, y] b[x2, y] c[x2, y] k[x1] r[x2] \right), \right.$$

$$m2 \rightarrow - \left( b[x1, y] c[x1, y] (b[x2, y] r[x1] - b[x1, y] r[x2]) + \right.$$

$$\left. \left. d[y] \left( - \frac{a[x1, x1] b[x2, y] r[x1]}{k[x1]} + \frac{a[x2, x1] b[x1, y] r[x2]}{k[x2]} \right) \right) / \right.$$

$$\left. \left( -b[x2, y] c[x2, y] \left( - \frac{a[x1, x1] b[x2, y] r[x1]}{k[x1]} + \frac{a[x2, x1] b[x1, y] r[x2]}{k[x2]} \right) + \right. \right.$$

$$\left. \left. b[x1, y] c[x1, y] \left( - \frac{a[x1, x2] b[x2, y] r[x1]}{k[x1]} + \frac{a[x2, x2] b[x1, y] r[x2]}{k[x2]} \right) \right) \right\}$$

---

```

m1[{x1_, x2_, y_}] :=
  - (a[x1, x2] b[x2, y] d[y] k[x2] r[x1] - b[x2, y]^2 c[x2, y] k[x1] k[x2] r[x1] -
    a[x2, x2] b[x1, y] d[y] k[x1] r[x2] +
    b[x1, y] b[x2, y] c[x2, y] k[x1] k[x2] r[x2]) /
  (-a[x1, x2] b[x1, y] b[x2, y] c[x1, y] k[x2] r[x1] +
    a[x1, x1] b[x2, y]^2 c[x2, y] k[x2] r[x1] +
    a[x2, x2] b[x1, y]^2 c[x1, y] k[x1] r[x2] -
    a[x2, x1] b[x1, y] b[x2, y] c[x2, y] k[x1] r[x2]);
m2[{x1_, x2_, y_}] := m1[{x2, x1, y}];
nn[{x1_, x2_, y_}] :=
  - (-a[x1, x2] a[x2, x1] d[y] r[x1] r[x2] +
    a[x1, x1] a[x2, x2] d[y] r[x1] r[x2] -
    a[x2, x2] b[x1, y] c[x1, y] k[x1] r[x1] r[x2] +
    a[x2, x1] b[x2, y] c[x2, y] k[x1] r[x1] r[x2] +
    a[x1, x2] b[x1, y] c[x1, y] k[x2] r[x1] r[x2] -
    a[x1, x1] b[x2, y] c[x2, y] k[x2] r[x1] r[x2]) /
  (-a[x1, x2] b[x1, y] b[x2, y] c[x1, y] k[x2] r[x1] +
    a[x1, x1] b[x2, y]^2 c[x2, y] k[x2] r[x1] +
    a[x2, x2] b[x1, y]^2 c[x1, y] k[x1] r[x2] -
    a[x2, x1] b[x1, y] b[x2, y] c[x2, y] k[x1] r[x2]);

```

---

#### Parameter values and functions

---

```

r[x_] := 1;

k[x_] := e-x2;

a[x1_, x2_] := e-α (x1-x2)2; α = 0.5;

b[x_, y_] := β1 e-β2 (x-y-p)2; β1 = 100; β2 = 0.2; p = Log[0.5];

c[x_, y_] := γ ex-y; γ = 0.2;

d[y_] := δ1 e-δ2 y; δ1 = 1; δ2 = 1;

```

---

## Invasion fitness

Prey invasion fitness and its derivatives

---

```

sPreydi [{x1_, x2_, y_}, X_] :=
  r[X]  $\left( 1 - \frac{a[X, x1] m1[{x1, x2, y}] + a[X, x2] m2[{x1, x2, y}]}{k[X]} \right) -$ 
  b[X, y] nn[{x1, x2, y}];

d1sPreydi [{x1_, x2_, y_}] :=  $\partial_x$  sPreydi [{x1, x2, y}, X] /. {X → x1};
d2sPreydi [{x1_, x2_, y_}] :=  $\partial_x$  sPreydi [{x1, x2, y}, X] /. {X → x2};
dd1sPreydi [{x1_, x2_, y_}] :=  $\partial_{x,x}$  sPreydi [{x1, x2, y}, X] /. {X → x1};
dd2sPreydi [{x1_, x2_, y_}] :=  $\partial_{x,x}$  sPreydi [{x1, x2, y}, X] /. {X → x2};

```

---

Predator invasion fitness and its derivatives:

---

```

sPreddi [{x1_, x2_, y_}, Y_] :=
  c[x1, Y] b[x1, Y] m1[{x1, x2, y}] + c[x2, Y] b[x2, Y] m2[{x1, x2, y}] - d[Y];

dsPreddi [{x1_, x2_, y_}] :=  $\partial_Y$  sPreddi [{x1, x2, y}, Y] /. {Y → Y};
ddsPreddi [{x1_, x2_, y_}] :=  $\partial_{Y,Y}$  sPreddi [{x1, x2, y}, Y] /. {Y → Y};

```

---

## Canonical equation

Deterministic drift

---

```

driftdi [{x1_, x2_, y_}] :=
   $\left\{ \frac{1}{2} \mu_{\text{Prey}} \sigma_{\text{Prey}}^2 m1[{x1, x2, y}] d1s_{\text{Prey}_{\text{di}}} [{x1, x2, y}], \right.$ 
   $\frac{1}{2} \mu_{\text{Prey}} \sigma_{\text{Prey}}^2 m2[{x1, x2, y}] d2s_{\text{Prey}_{\text{di}}} [{x1, x2, y}],$ 
   $\left. \frac{1}{2} \mu_{\text{Pred}} \sigma_{\text{Pred}}^2 nn[{x1, x2, y}] ds_{\text{Pred}_{\text{di}}} [{x1, x2, y}] \right\};$ 

```

---

Stream plot (note below that the boundaries of the mutual invadability cone are attracting, and so the cone is not forward invariant under the CE)

---

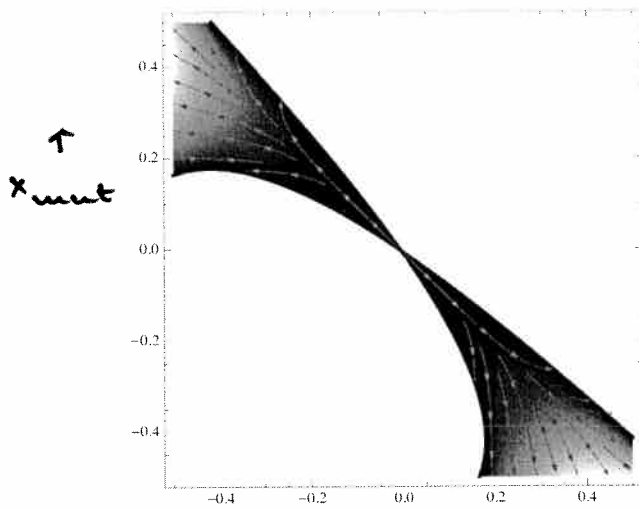
```

CEstream =
  StreamPlot[
    If[m1[{x1, x2, 0.69}] > 0 && m2[{x1, x2, 0.69}] > 0 && Abs[x1 - x2] > 0.01,
      driftdi[{x1, x2, 0.69}][[1 ;; 2]], {0, 0}], {x1, -0.5, 0.5},
      {x2, -0.5, 0.5}];

Show[MIPint, MIPbnd, CEstream]

```

---



~~all~~  
 $x_{mut} \rightarrow$

## Deterministic evolutionary tree

---

```

v0 = {1.5, 4.5}; (* starting point of orbit *)
t0 = 0; (* start time *)
t∞ = 750 000; (* stop time *)
Δt = 50; (* integration time step *)

(* positional date *)
xdata = {};
ydata = {};

(* stability data ES/NES *)
xstab = {};
ystab = {};

(* monomorphic part of the tree; note the extra stopping condition *)
v = v0;
t = t0;
While[t ≤ t∞ && n[v] > 0 &&
  dsPreymo[v - σPrey {0.001, 0}] dsPreymo[v + σPrey {0.001, 0}] > 0,
  xdata = Join[xdata, {{v[[1]], t}}];
  ydata = Join[ydata, {{v[[2]], t}}];
  xstab = Join[xstab, {{ddsPreymo[v], t}}];
  ystab = Join[ystab, {{ddsPredmo[v], t}}];
  v = v + Δt driftmo[v];
  t = t + Δt;
];

(* dimorphic part of the tree *)
v = {v[[1]] - 0.01 σPrey, v[[1]] + 0.01 σPrey, v[[2]]};
While[t ≤ t∞ && m1[v] > 0 && m2[v] > 0 && nn[v] > 0,
  xdata = Join[xdata, {{v[[1]], t}, {v[[2]], t}}];
  ydata = Join[ydata, {{v[[3]], t}}];
  xstab = Join[xstab, {{ddl1sPreydi[v], t}, {dd2sPreydi[v], t}}];
  ystab = Join[ystab, {{ddsPreddi[v], t}}];
  v = v + Δt driftdi[v];
  t = t + Δt;
];

```

---

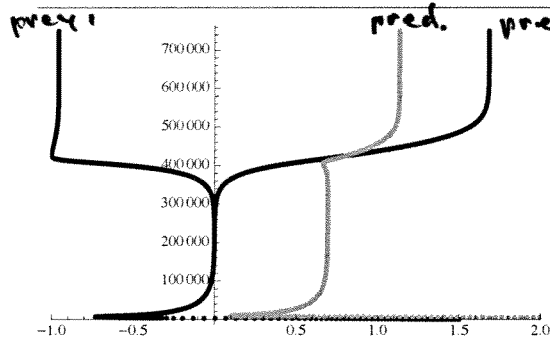


## Trait values

---

```
xtree = ListPlot[xdata, PlotStyle -> {Black}, Joined -> False];
ytree = ListPlot[ydata, PlotStyle -> {Red}, Joined -> False];
Show[xtree, ytree, PlotRange -> {{-1, 2}, All}]
```

---

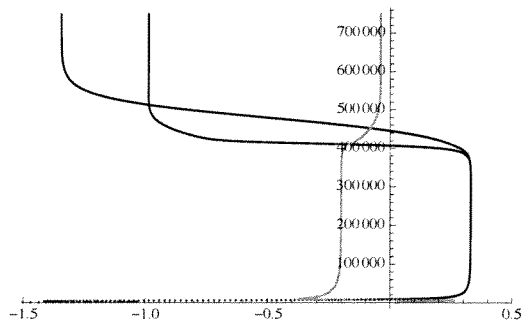


## Stability data

---

```
xstree = ListPlot[xstab, PlotStyle -> {Black, PointSize[0.002]},
  Joined -> False];
ystree = ListPlot[ystab, PlotStyle -> {Red, PointSize[0.002]},
  Joined -> False];
Show[xstree, ystree, PlotRange -> {{-1.5, 0.5}, All}]
```

---



*Conclusion: after branching in the prey species, the population evolves to an evolutionarily stable point with two prey types and one predator type. However, as the mutual invadability cone is not forward invariant (see above) stochastic orbits may readily leave the cone so that branching may fail. For sufficiently small mutation step sizes, however, there is a positive probability of not leaving the cone, and so there is a positive probability of branching. Since after failed branching the population will be in the neighborhood of the singular point, branching will occur sooner or later with probability one. The time till successful branching should be exponentially distributed and may be very long. This phenomenon has been dubbed "evolutionary loitering" (pc. Eva Kisdi).*