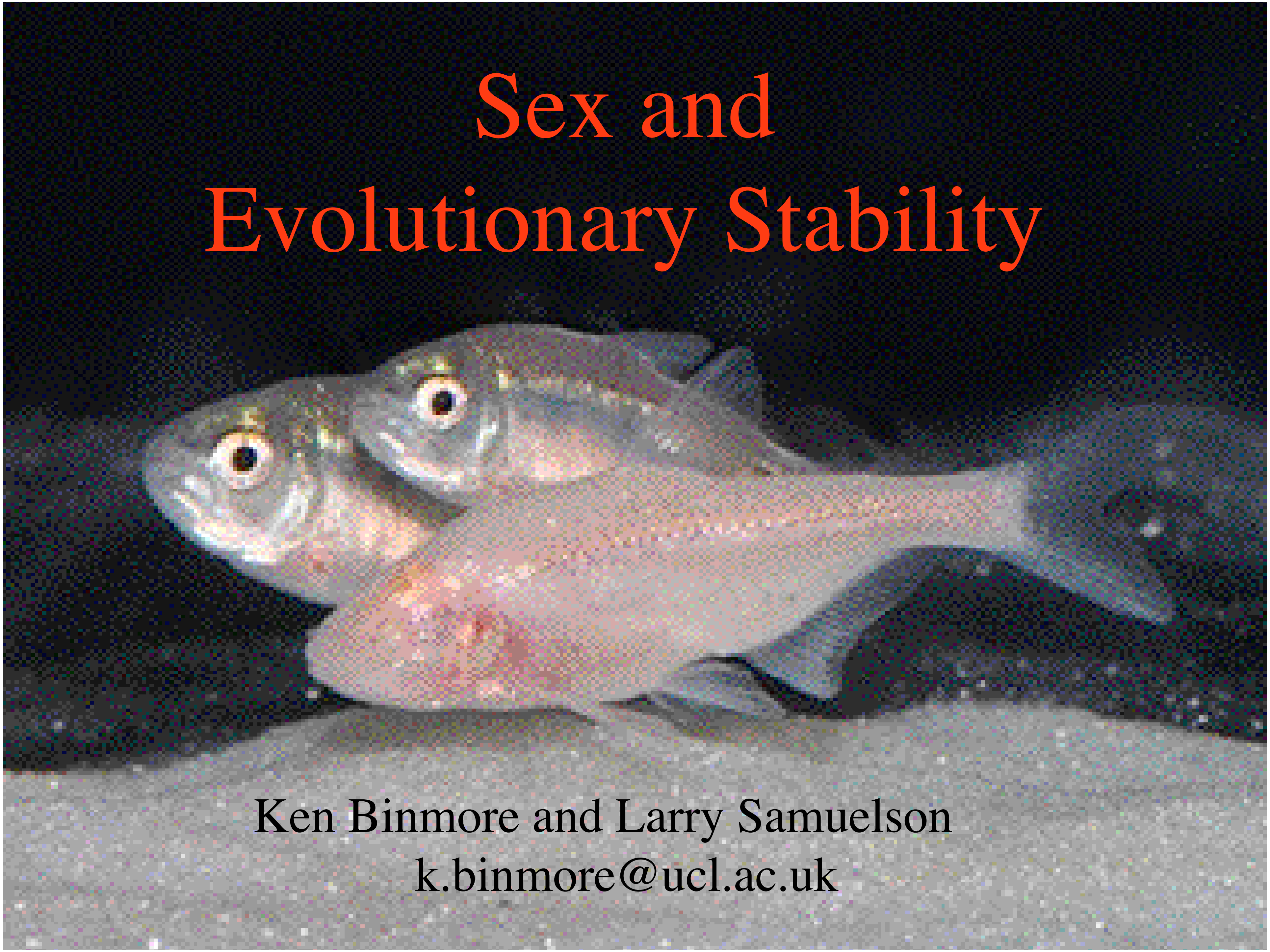
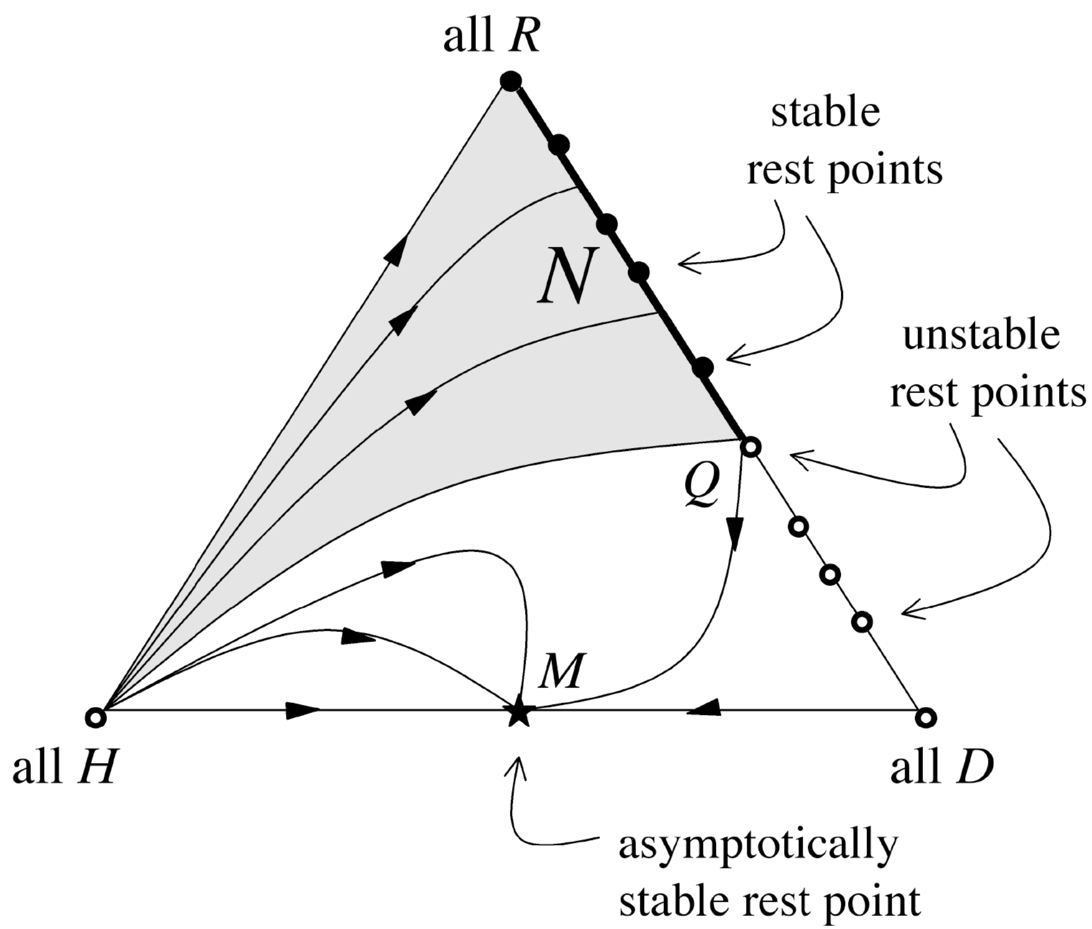
Sex and Evolutionary Stability

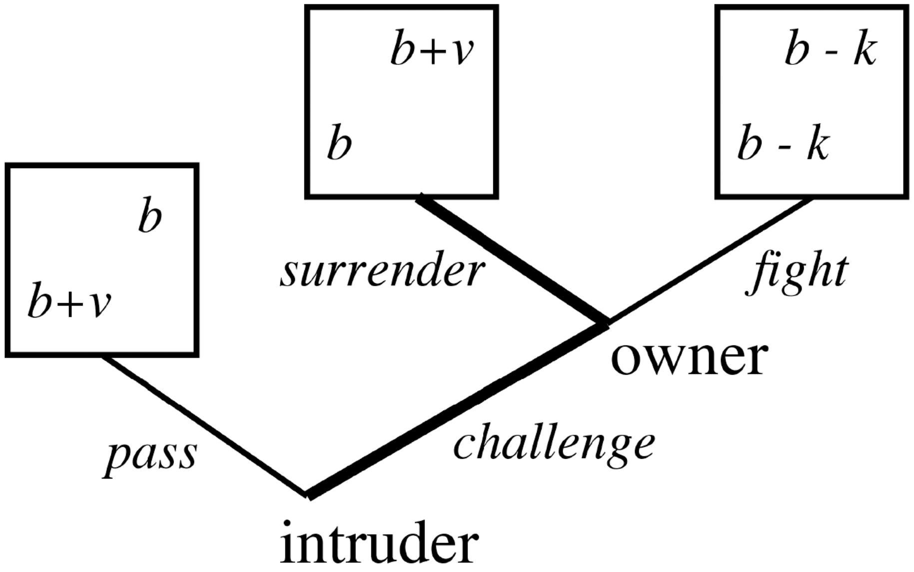


Ken Binmore and Larry Samuelson
k.binmore@ucl.ac.uk

	D	*H*	*R*
D	1 1	2 0	1 1
H	0 2	-1 -1	-1 -1
R	1 1	-1 -1	1 1



Hawk/Dove/Retaliator Game



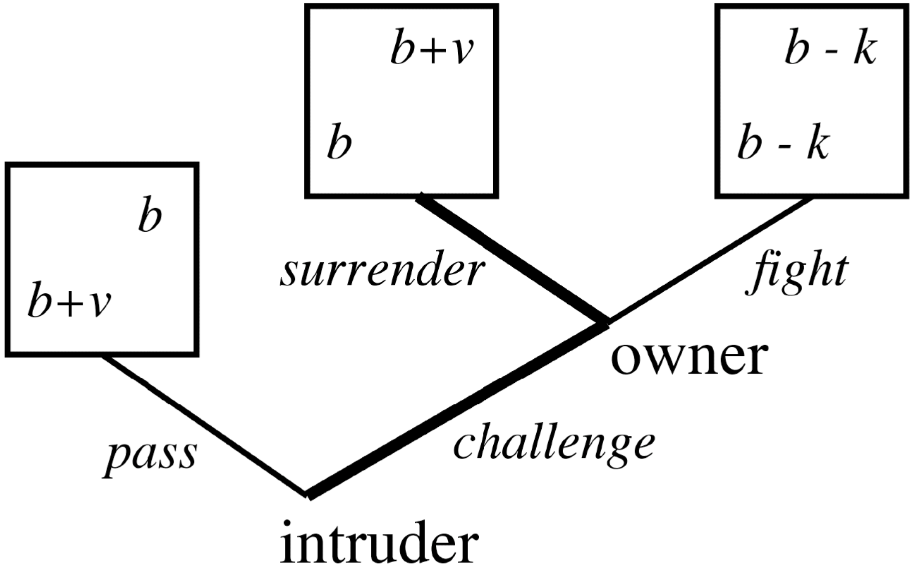
extensive form

Resource Game

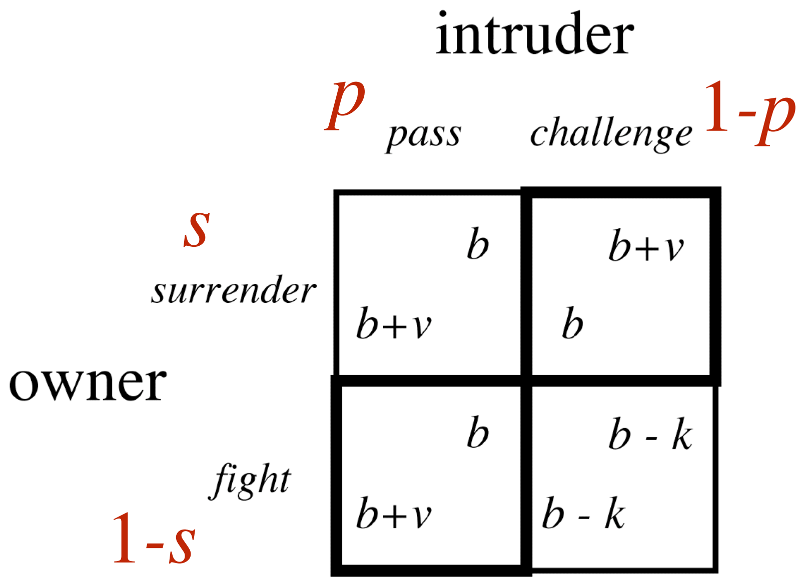
		intruder: *pass*	intruder: *challenge*
owner	*surrender*	b (intruder), $b+v$ (owner)	$b+v$ (intruder), b (owner)
	fight	b (intruder), $b+v$ (owner)	$b - k$ (intruder), $b - k$ (owner)

strategic form

$0 < k < b$



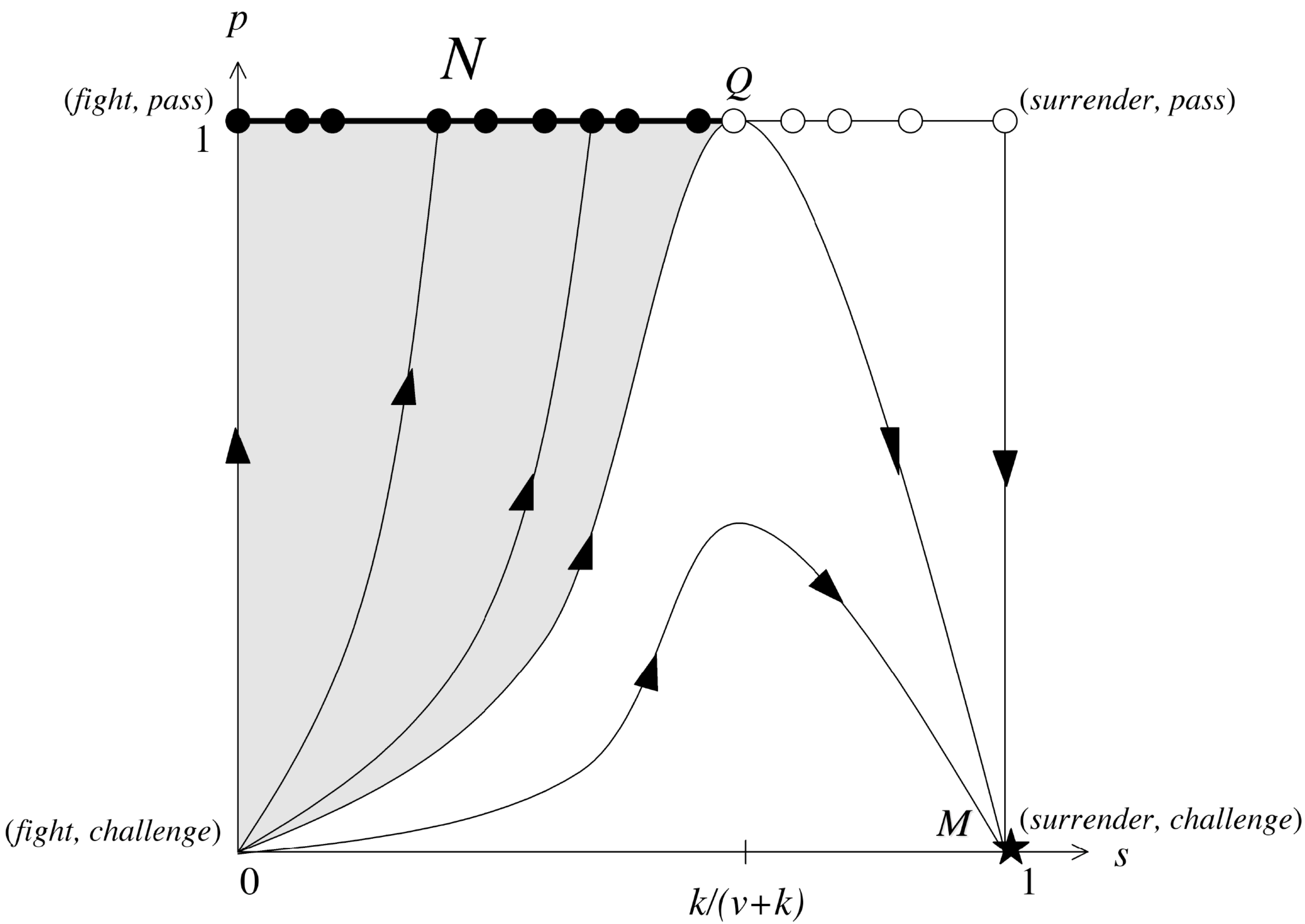
extensive form



strategic form

$$\dot{s} = s(\pi_S - \overline{\pi}_O) = ks(1-s)(1-p)$$

$$\dot{p} = p(\pi_P - \overline{\pi}_I) = p(1-p)(k - s(v+k))$$



p
N
Q
(fight, pass)
1
(surrender, pass)
(fight, challenge)
M
(surrender, challenge)
s
0
k/(v+k)
1

$$\dot{s} = s(\pi_S - \overline{\pi}_O) + \mu_F(1 - s)\pi_F - \mu_S s \pi_S$$

$$\dot{p} = p(\pi_P - \overline{\pi}_I) + \mu_C(1 - p)\pi_C - \mu_P p \pi_P$$

drift terms

$$\dot{s} = s(\pi_S - \overline{\pi}_O) + \mu_F(1-s)\pi_F - \mu_S s \pi_S$$

$$\dot{p} = p(\pi_P - \overline{\pi}_I) + \underbrace{\mu_C(1-p)\pi_C - \mu_P p \pi_P}_{\text{drift terms}}$$

$$\frac{s(1-s)(1-p)k}{p(1-p)[k - s(v+k)]} = \frac{\mu_S s \pi_s - \mu_F(1-s)\pi_F}{\mu_P p \pi_P - \mu_C(1-p)\pi_C}$$

$$\mu_P = (1-\beta)\delta_I \qquad \mu_C = \beta\delta_I \qquad \alpha = \beta = \frac{1}{2},$$

$$\mu_S = (1-\alpha)\delta_C \qquad \mu_F = \alpha\delta_O$$

$$\dot{s} = s(\pi_S - \overline{\pi}_O) + \mu_F(1-s)\pi_F - \mu_S s \pi_S$$

$$\dot{p} = p(\pi_P - \overline{\pi}_I) + \mu_C(1-p)\pi_C - \mu_P p \pi_P$$

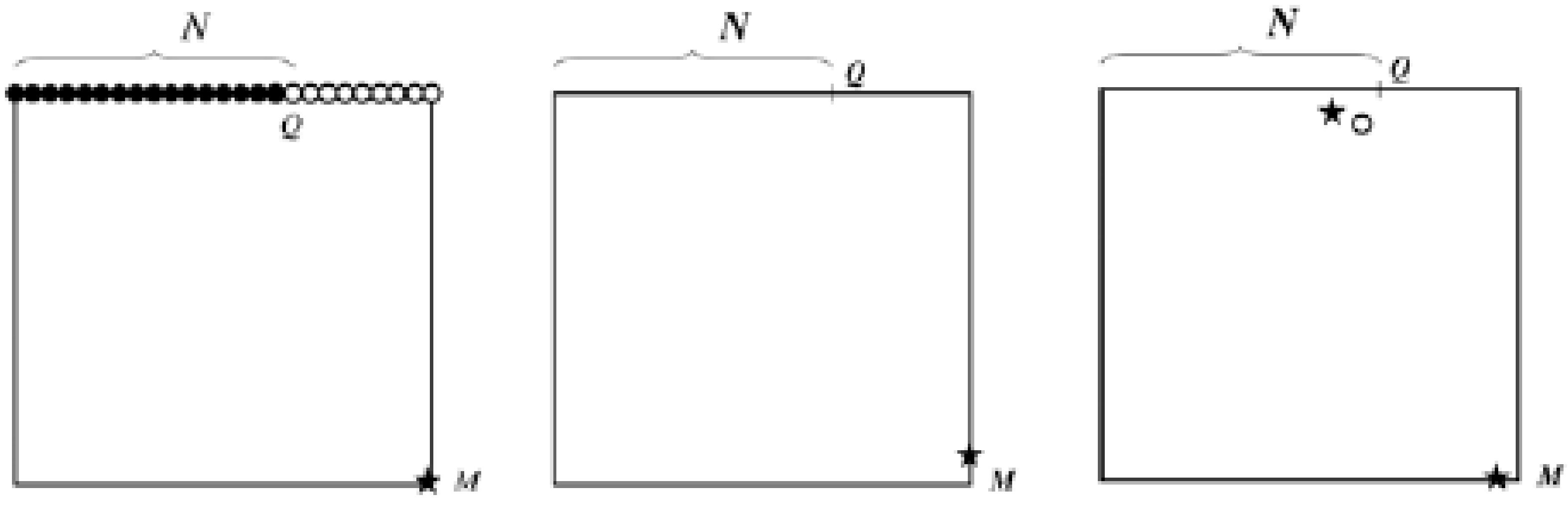
drift terms

$$s^* = k/(k+v)$$

$$\frac{s s^* (1-s)}{2(s-\frac{1}{2})(s^*-s)} = \frac{b+v}{b}\frac{\delta_O}{\delta_I}$$

>1 ?

background fitness



(a) No mutation

(b) All mutation from aggressive to passive

(c) Mutation both ways (δ_O/δ_I small)

Figure 4: Stability with different assumptions on mutation rates. Figure 4(a) reproduces the configuration of rest points from Figure 3, for the case of asexual dynamics without drift. Figure 4(b) shows that only the asymptotic attractor M survives when we allow only mutations from aggressive to passive behavior. Figures 4(c) illustrates the case when the probability that an aggressive allele mutates to a passive allele is the same as the probability of a mutation in the other direction. These rates may differ between the owner and intruder loci, with $\mu_S = \mu_F = \frac{1}{2}\delta_O$ and $\mu_P = \mu_C = \frac{1}{2}\delta_I$. Note that rest points near N occur in pairs: an asymptotic attractor marked with a star and a saddle point marked with a circle.

Sexual Dynamics

measure of aa gametes

genotype	population proportion	gametes per individual	successful a gametes	successful A gametes
aa	x	π_{aa}	$(1-\mu_a)X$	$\mu_a X$
aA or Aa	y	π_{aA}	$\frac{1}{2}(1-\mu_a)Y + \frac{1}{2}\mu_A Y$	$\frac{1}{2}\mu_a Y + \frac{1}{2}(1-\mu_A)Y$
AA	z	π_{AA}	$\mu_A Z$	$(1-\mu_A)Z$

genotype	probability that an offspring is of this genotype
aa	$(X+\frac{1}{2}Y+d)^2/\overline{\pi}^2$
aA or Aa	$2(X+\frac{1}{2}Y+d)(Z+\frac{1}{2}Y-d)/\overline{\pi}^2$
AA	$(Z+\frac{1}{2}Y-d)^2/\overline{\pi}^2$

$$\mu_A Z - \mu_a X + \tfrac{1}{2}Y(\mu_A - \mu_a)$$

$$\overline{\pi} = X + Y + Z$$

Sexual Dynamics

$$x(t+\tau) = \frac{x(t) + \tau\frac{1}{2}\overline{\pi}\,(X + \frac{1}{2}Y + d)^2/\overline{\pi}^2}{1 + \tau\frac{1}{2}\overline{\pi}}$$

$$y(t+\tau) = \frac{y(t) + \tau\frac{1}{2}\overline{\pi}\,2(X + \frac{1}{2}Y + d)(Z + \frac{1}{2}Y - d)/\overline{\pi}^2}{1 + \tau\frac{1}{2}\overline{\pi}}$$

$$z(t+\tau) = \frac{z(t) + \tau\frac{1}{2}\overline{\pi}\,(Z + \frac{1}{2}Y - d)^2/\overline{\pi}^2}{1 + \tau\frac{1}{2}\overline{\pi}}.$$

Sexual Dynamics

$$x + y + z = 1,$$

$$\begin{aligned}
\dot{x} &= (2X + Y + 2d)^2/\overline{\pi} - 4\overline{\pi}x \\
\dot{z} &= (2Z + Y - 2d)^2/\overline{\pi} - 4\overline{\pi}z
\end{aligned}$$

Sexual Dynamics

$$x + y + z = 1,$$

$$\begin{aligned} \dot{x} &= (2X + Y + 2d)^2/\overline{\pi} - 4\overline{\pi}x \\ \dot{z} &= (2Z + Y - 2d)^2/\overline{\pi} - 4\overline{\pi}z \end{aligned}$$

At a rest point where $\dot{x} = \dot{z} = 0$,

$$\begin{aligned} (2X + Y + 2d)^2 &= 4x\overline{\pi}^2\,, \\ (2Z + Y - 2d)^2 &= 4z\overline{\pi}^2\,. \end{aligned}$$

When it is right to take the positive square roots, we obtain

$$2(X + Y + Z) = 2\overline{\pi}(\sqrt{x} + \sqrt{z})\,,$$

from which we derive the useful equations:

$$\begin{aligned} \sqrt{x} + \sqrt{z} &= 1 \\ y &= 2\sqrt{xz} \end{aligned}$$

Sexual Dynamics: Hawk-Dove Game

To accommodate sexual reproduction, assume that the allele a is recessive and that A is dominant. The strategy *dove* is played by the genotype aa. The strategy *hawk* is played by both genotypes aA and AA. We then have that $\pi_{aa} = \pi_D$ and $\pi_{aA} = \pi_{AA} = \pi_H$. Writing (6) and (7) into equation (4), we obtain that

$$x(1 - \sqrt{x})(\pi_D - \pi_H) + d = 0, \tag{8}$$

where x is the proportion of the population playing *dove*. Apart from the drift term d, this equation differs from that obtained using the standard asexual replicator dynamics only in replacing the factor $1 - x$ by $1 - \sqrt{x}$.

In the absence of drift ($d = 0$), either $x = 0$ or $x = 1$ or else

$$\pi_H = \pi_D ,$$

which is the equation that determines the mixed Nash equilibrium in which *dove* is played with probability $x = \frac{1}{2}$ and *hawk* is played with probability $y + z = 1 - x = \frac{1}{2}$. This matches the outcome under asexual dynamics and provides an illustration of Grafen's [7] general observation that the rest points are the same in both the sexual and the asexual dynamics. The frequency of the aa genotype at the mixed equilibrium is therefore $x = 0.5$. It follows from equations (6) and (7) that the frequencies of the aA and AA genotypes are respectively $y = 0.415$ and $z = 0.086$.

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phenotypical gambit

Impact of Sexual Transmission on Drift

genotype	aa	aA	AA	bb	bB	BB
phenotype	*surrender*	*fight*	*fight*	*pass*	*challenge*	*challenge*

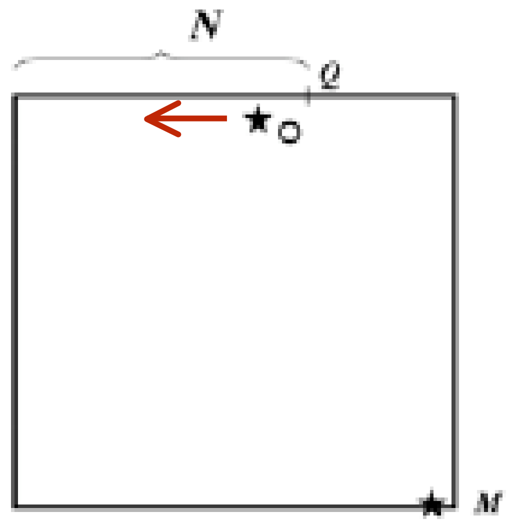
$$
\begin{aligned}
s(1-\sqrt{s})(1-p)k + d_O &= 0\,, \\
p(1-\sqrt{p})(k - s(v+k)) + d_I &= 0\,,
\end{aligned}
$$

where the drift terms are given by

$$
\begin{aligned}
d_O &= (b + pv - k(1-p))(1-\sqrt{s})(\mu_A - \mu_a\sqrt{s}) - \mu_a(b+pv)s \\
d_I &= (b + s(v+k) - k)(1-\sqrt{p})(\mu_B - \mu_b\sqrt{p}) \;\; - \mu_b bp\,.
\end{aligned}
$$

Impact of Sexual Transmission on Drift

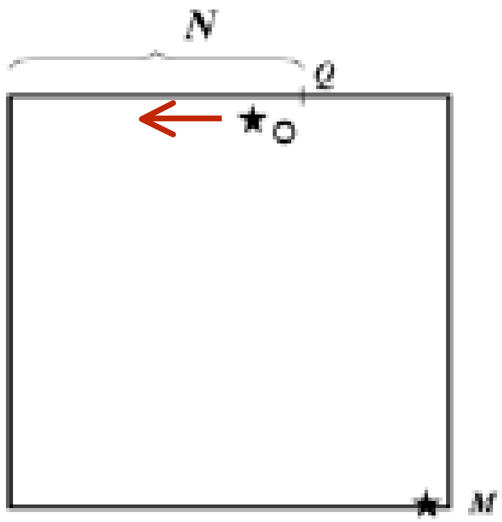
$$\frac{ss^*(1-s)}{2(s-\frac{1}{2})(s^*-s)} = \frac{b+v}{b}\frac{\delta_O}{\delta_I}\frac{(\sqrt{s}-\frac{1}{2})(1-s)}{2(s-\frac{1}{2})(1-\sqrt{s})} \quad >1\ ?$$



(c) Mutation both ways

Impact of Sexual Transmission on Drift

$$\frac{ss^*(1-s)}{2(s-\frac{1}{2})(s^*-s)} = \frac{b+v}{b}\frac{\delta_O}{\delta_I}\frac{(\sqrt{s}-\frac{1}{2})(1-s)}{2(s-\frac{1}{2})(1-\sqrt{s})}$$ >1 ?



(c) Mutation both ways

Hardy-Weinberg