# Biological Applications of Game Theory

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1st Joint China-Dutch Seminar on Game Theory
and 4th China Meeting on Game Theory and its Applications

**Maastricht University**
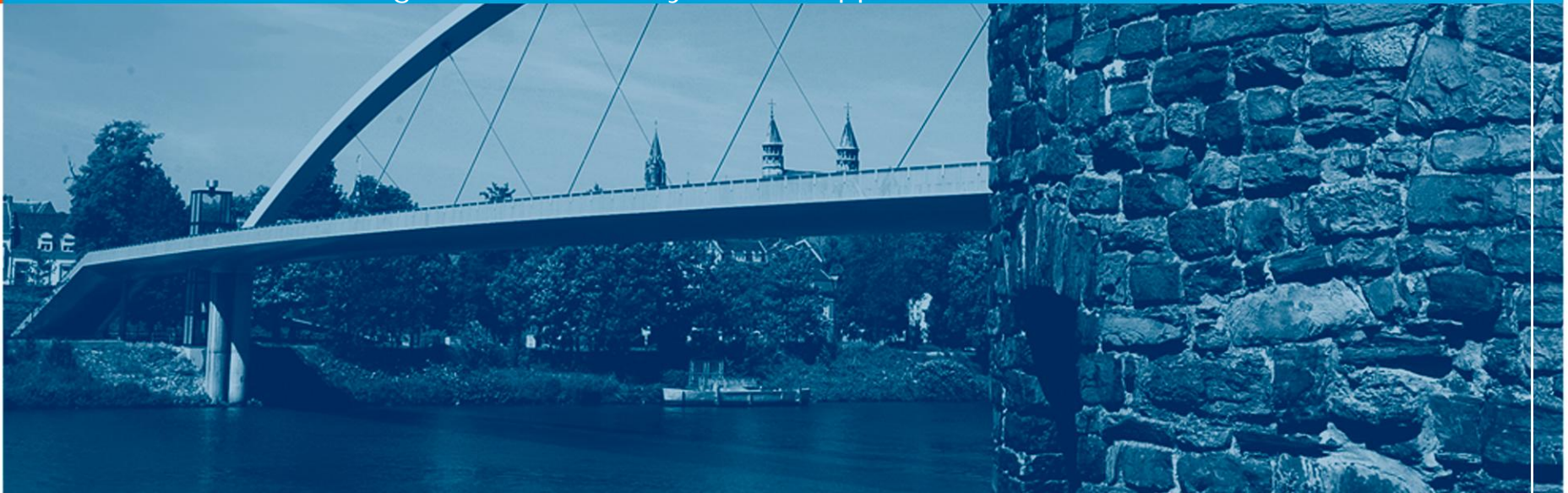
# Presentation Outline

Two examples of *Biological Applications* of Game Theory:

- *Foraging bees*, matching and Nash equilibrium
- *Sex of trees* and evolutionary stable strategies

Some remarks on work in progress

# Foraging Bees, Matching and Nash Equilibrium



Frank Thuijsman, Bezalel Peleg, Mor Amitai, Avi Shmida:
Automata, matching and foraging behavior of bees.
*Journal of Theoretical Biology* 175, 1995.

# Outline of Paper

Two approaches that explain certain observations of foraging behavior:

- The Ideal Free Distribution (IFD)
- The Matching Law (ML)
- Risk Averse Behaviour

One approach based on an '$\varepsilon$-sampling' strategy another based on automata involving 'failures'.

Today we restrict to $\varepsilon$-sampling

# The Ideal Free Distribution

Individual foragers distribute themselves over various patches proportional to the amounts of resources available in each.

## Many foragers

For example: if patch *A* contains twice as much food as patch *B*, then there will be twice as many individuals foraging in patch *A* as in patch *B*.

Stephen Fretwell & Henry Lucas: On territorial behaviour and other factors influencing habitat distribution in birds, *Acta Biotheoretica* 19, 1970.
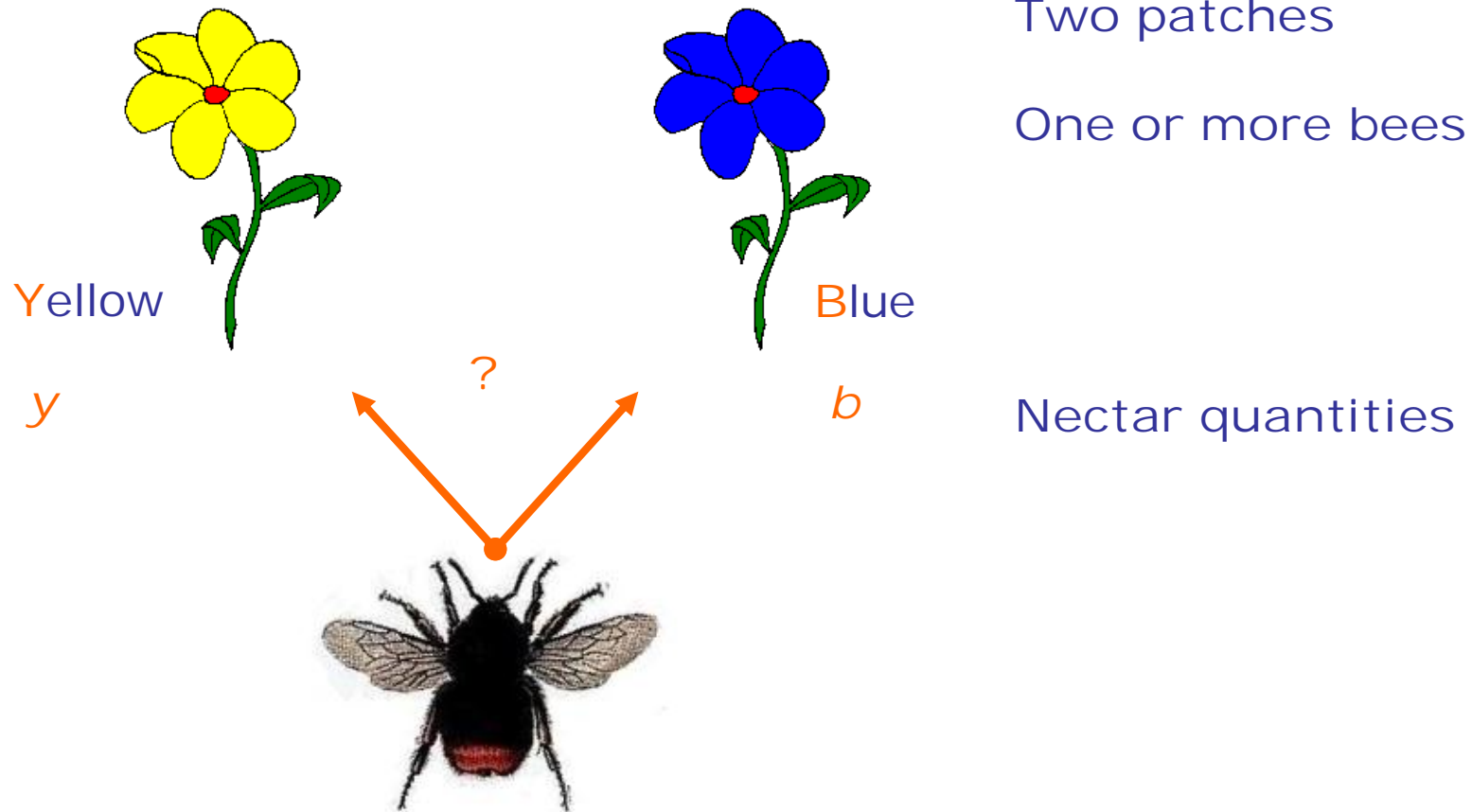
# The Matching Law

The organism allocates its behavior over various activities
in proportion to the value derived from each activity.
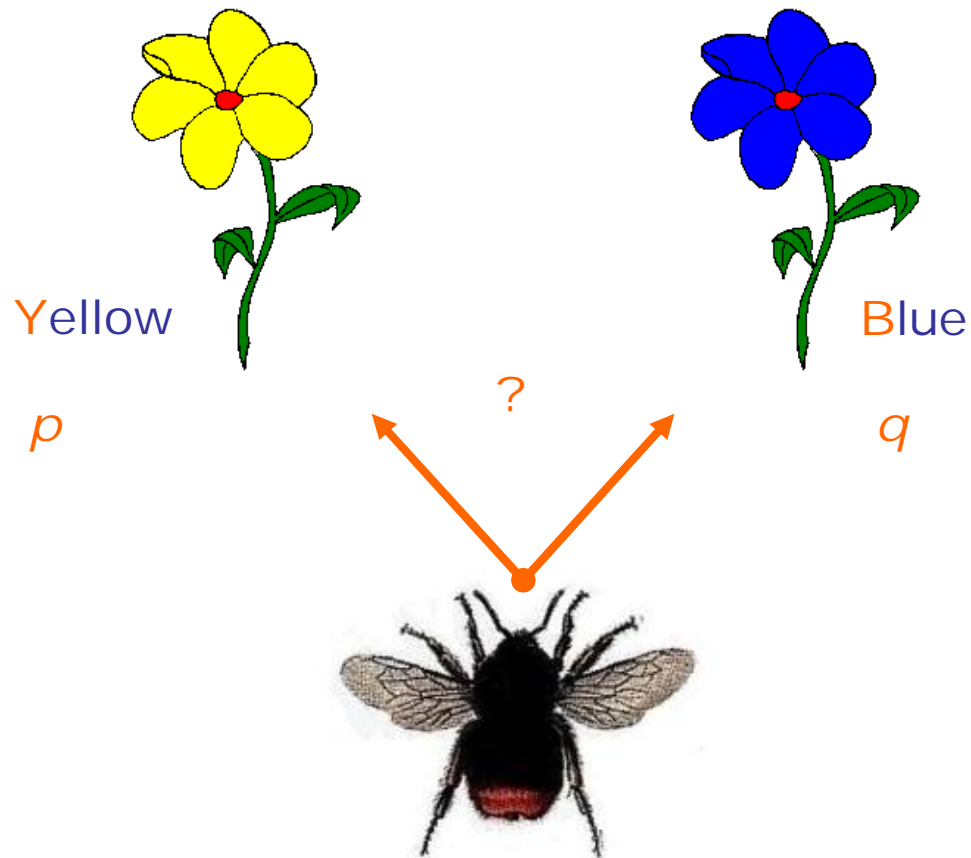
## Single forager

For example: if the probability of finding food in patch $A$
is twice as much as in patch $B$, then the foraging individual
will visit patch $A$ twice as often as patch $B$.

Richard Herrnstein: On the law of effect, *Journal of the Experimental Analysis of Behavior* 13, 1970.

# Simplified Model

Yellow

*y*

?

Blue

*b*

Two patches

One or more bees

Nectar quantities

# Simplified Model

Yellow

$p$

?

Blue

$q$

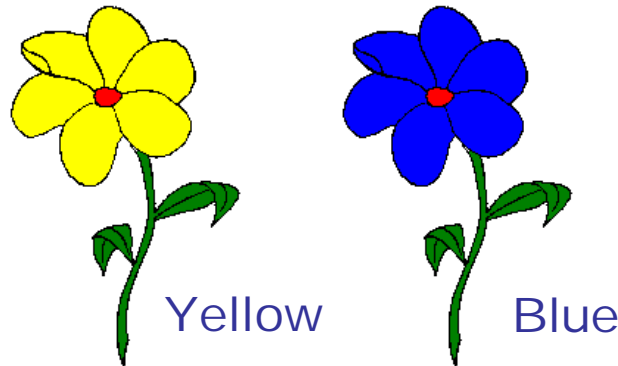Two patches

One or more bees

Nectar probabilities

# IFD and Simplified Model

two patches:                      Yellow            Blue
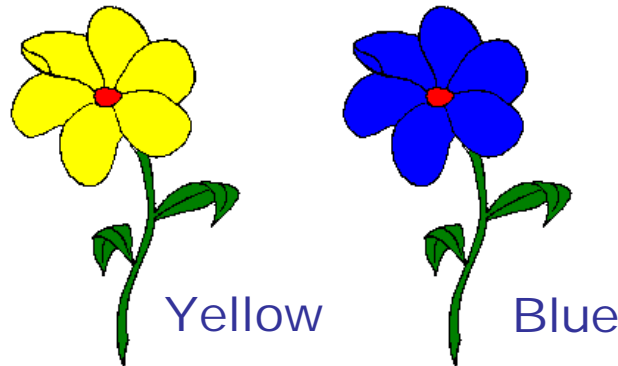
nectar quantities:          $y$                      $b$

number of bees:            $n_Y$                    $n_B$

Ideal Free Distribtion: $n_Y / n_B$ ⟶ $y / b$

# ML and Simplified Model

Yellow    Blue

two patches:

nectar probabilities:    $p$    $q$

# visits by one bee:    $n_Y$    $n_B$

Matching Law:    $n_Y / n_B$  ⟶  $p / q$

# The $\varepsilon$-Sampling Strategy

Start by choosing a color at random
At each following stage:
   with probability $\varepsilon$ sample *other* color
   with probability 1 - $\varepsilon$ stay at *same* color.

If sample "at least as good",
   then stay at new color,
   otherwise return immediately.

$\varepsilon > 0$

# IFD, $\varepsilon$-Sampling, Assumptions

- reward at *Y*ellow:      0 or 1 with average $y/n_Y$
  reward at *B*lue:        0 or 1 with average $b/n_B$
- no nectar accumulation
- the $\varepsilon$ is very small: at most one bee sampling at any stage
- at sampling the bee 'knows' $y/n_Y$ or $b/n_B$ (critical level)

# $\varepsilon$-Sampling gives IFD

Proof:

Let $P(n_Y, n_B) = y \cdot (1 + 1/2 + 1/3 + \cdots + 1/n_Y)$

$\qquad\qquad\qquad - b \cdot (1 + 1/2 + 1/3 + \cdots + 1/n_B)$

If a bee moves from $Y$ to $B$,

then we go from $(n_Y, n_B)$ to $(n_Y - 1, n_B + 1)$

and $P(n_Y - 1, n_B + 1) - P(n_Y, n_B) = b/(n_B + 1) - y/n_Y > 0$

So $P$ is increasing at each *move*, until it reaches a maximum

At maximum $b/(n_B + 1) < y/n_Y$ and $y/(n_Y + 1) < b/n_B$
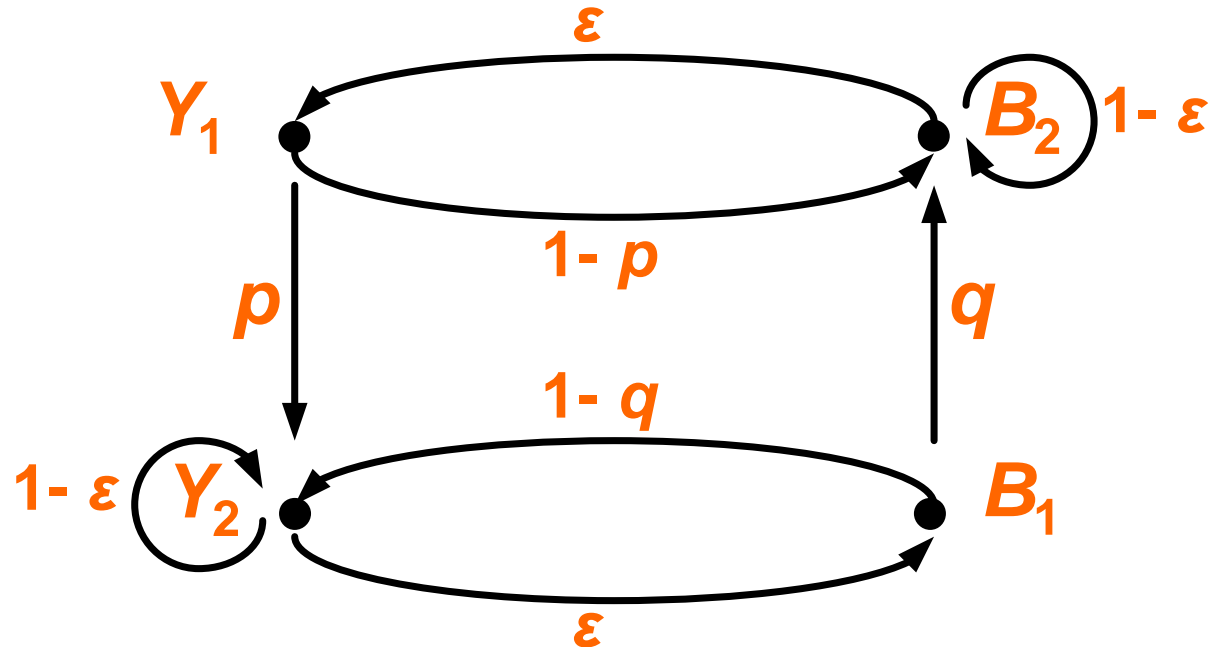
from which we conclude that $y/n_Y \approx b/n_B$

and so we find $\boxed{y/b \approx n_Y/n_B}$

# ML, $\varepsilon$-Sampling, Assumptions

- Bernoulli flowers: reward 0 or 1
- with probability $p$ and 1-$p$ resp. at $Y$
- with probability $q$ and 1-$q$ resp. at $B$
- no nectar accumulation
- the $\varepsilon > 0$ is very small
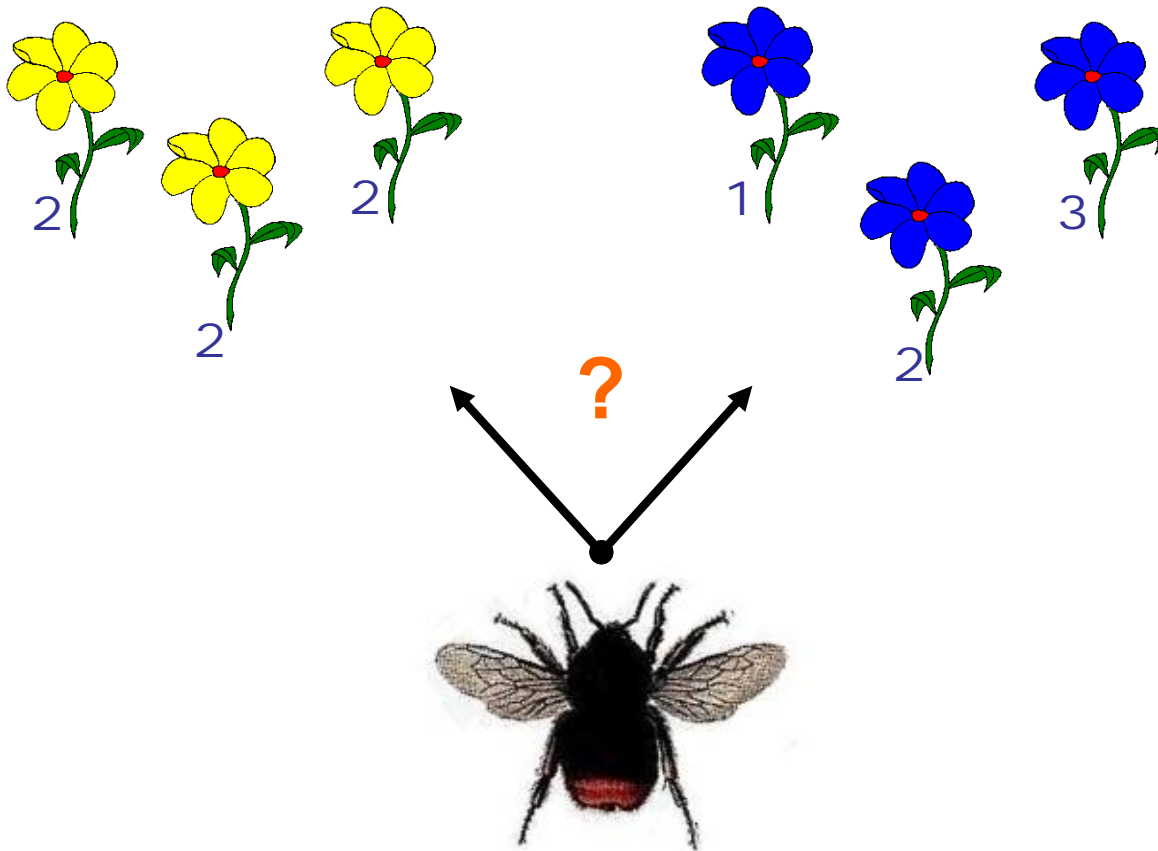- at sampling the bee 'knows' $p$ or $q$ (critical level)

# ML, $\varepsilon$-Sampling, Movements



By calculating the stationary distribution of this Markov chain:

$$n_Y/n_B = (p + q\varepsilon) / (q + p\varepsilon) \approx p/q$$

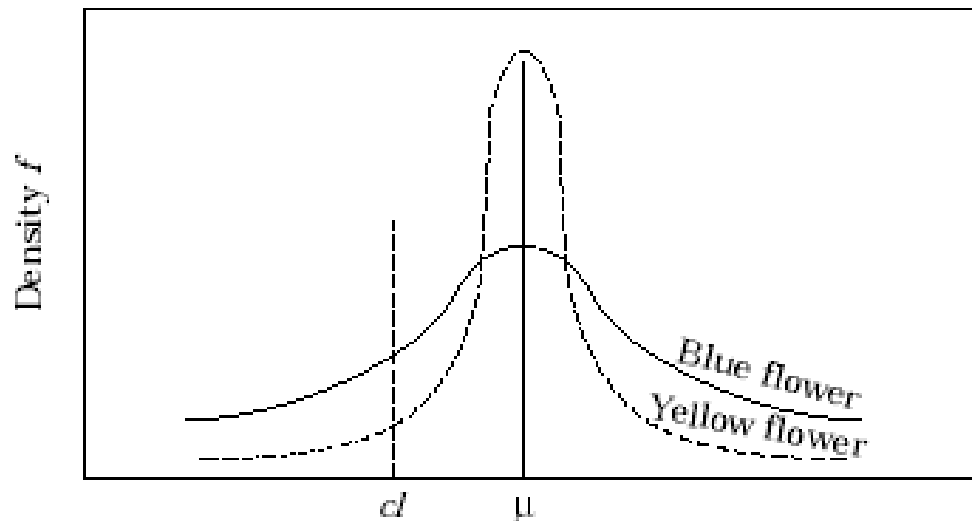# Attitude towards Risk

# Attitude towards Risk

Assuming normal distributions:

If the critical level is less than the mean,
then any probability matching forager will favour lower variance,
i.e. it seems to be risk averse

# Some Final Remarks on Foraging

- The $\varepsilon$-sampling result does not really depend on $\varepsilon$.
- The $\varepsilon$-sampling result also applies to more than two patches.
- The $\varepsilon$-sampling strategy requires staying in same color for a long time.
- The $\varepsilon$-sampling strategy can also be applied to traffic routing in congestion models.
- IFD and ML can also be obtained by a failures automaton
  (e.g. leave $Y$ after $r$ empty flowers, leave $B$ after $s$ empty ones).
- In order to achieve IFD or ML with a failures automaton, the parameters $r$ and $s$ have to be fine tuned on the available nectar quantities $y$ and $b$ (or reward probabilities $p$ and $q$).
- Field data support 'failures behavior'.

# Some Final Remarks on Matching

For non-zerosum repeated games  we know the procedure of
'fictitious play', where players are assumed at each stage
to play a best reply against the action frequencies observed thus far.
For fictitious play the joint distribution of actions generally
does not converge to a Nash-equilibrium.

However, if each player at each stage does 'regret matching',
then the joint distribution of actions does converge to the set
of correlated equilibria of the stage game.
(Sergiu Hart & Andreu Mas-Colell: A simple adaptive procedure
leading to correlated equilibrium, *Econometrica* 68, 2000)

# Sex of Trees and Evolutionary Stable Strategies



Tom de Jong, Avi Shmida, Frank Thuijsman:
Sex allocation in plants and the evolution of monoecy.
*Evolutionary Ecology Research* 10, 2008.
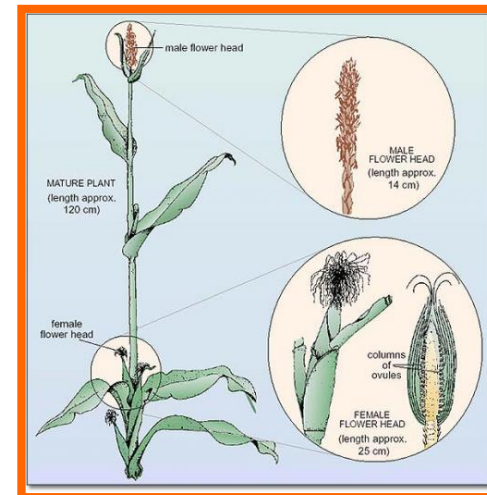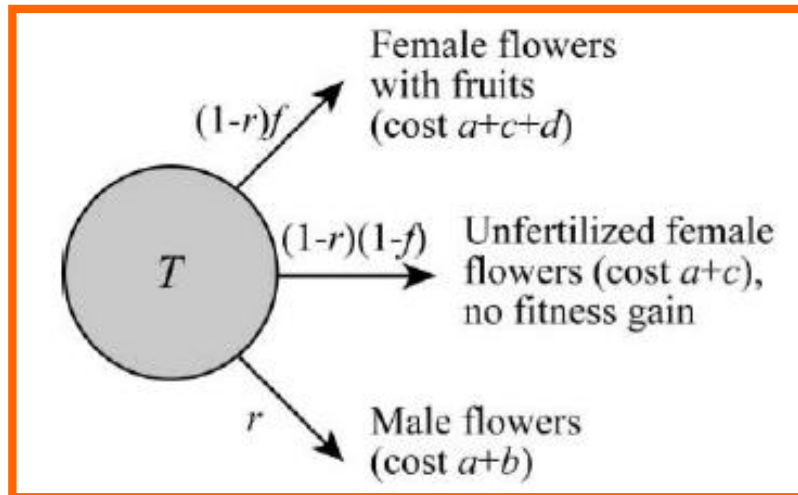
# Sex Systems of Plants

**Table 1.** Sex systems (%) in the flora of the Levant, which comprises Israel, Sinai, and Jordan ($n = 2916$ species), based on unpublished observations by A. Shmida

| | Description | Percent | Flower size (mm) (species average) |
|---|---|---|---|
| Hermaphrodite | All flowers male and female | 86.6 | 12.9 |
| Andromonoecy | Male and hermaphrodite flowers on the same plant | 5.7 | 3.5 |
| Gynomonoecy | Female and hermaphrodite flowers on the same plant | 0.4 | 1.7 |
| Monoecy | Separate male and female flowers on the same plant | 3.6 | 2.1 |
| Androdioecy | Male plants co-exist with hermaphrodite or monoecious plants | 0.06 | 2.5 |
| Gynodioecy | Female plants co-exist with hermaphrodite or monoecious plants | 0.3 | 19.3 |
| Dioecy | Male and female flowers on separate plants | 2.2 | 2.3 |
| Other | More complex systems | 1.1 | 1.8 |

# Hermaphrodite Plants



fruit seeds $\}$ $d$

stigma style ovary $\}$ $c$

nectar corolla $\}$ $a$

calyx

stamens $b$
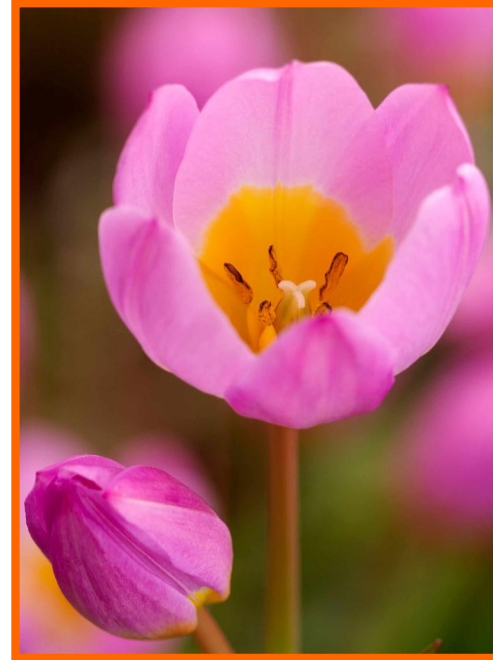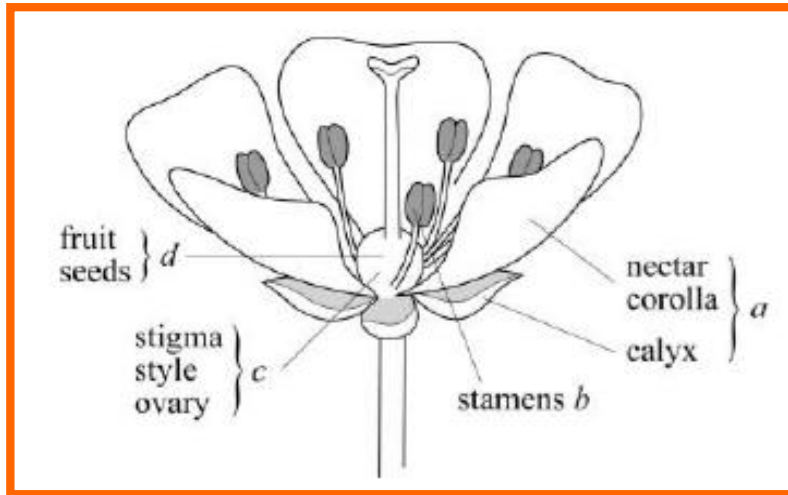
# Monoecious Plants





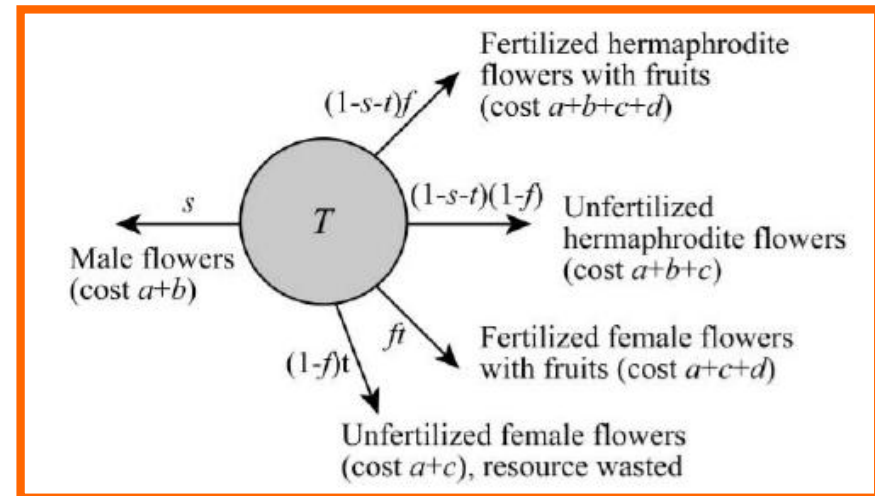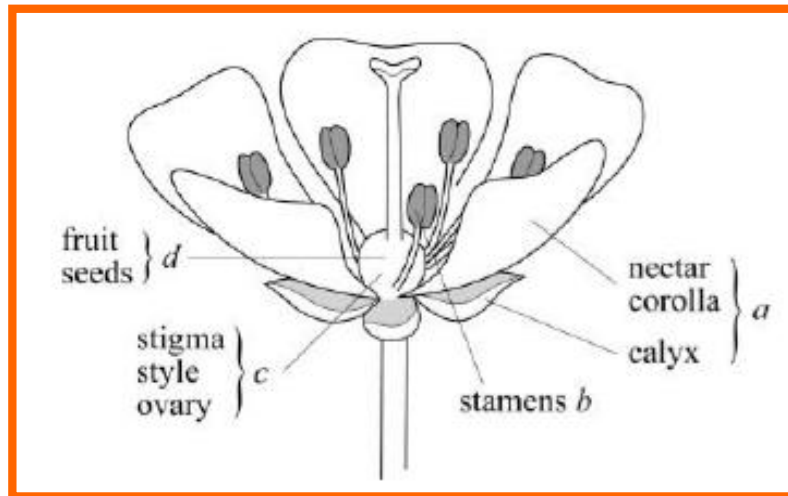Monoecious plants dominate vast parts of world vegetation:

Oak, beech, hornbeam, hazel, pine, fir, larch, walnut, …

# Sex of Trees and Evolutionary Stable Strategies

Question addressed in the paper:

Which ecological factors favour the transition

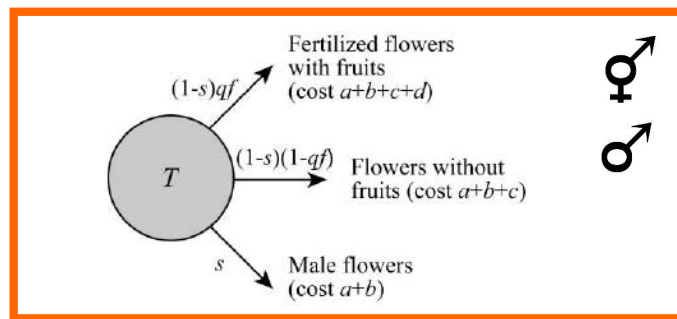from the hermaphrodite system to that of monoecy?

# Four Sex Systems Examined
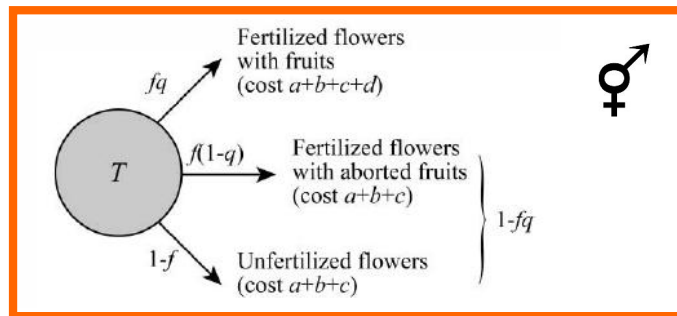


Hermaphrodite plants
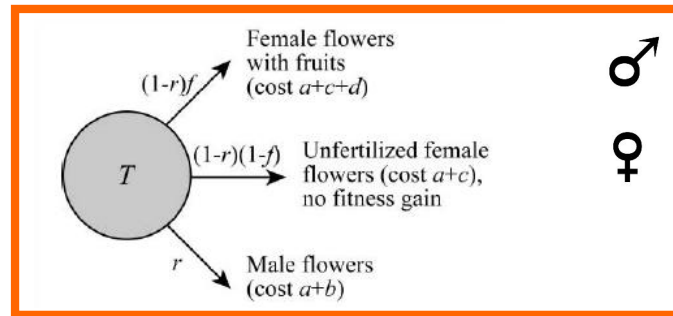


Monoecious plants



Andromonoecious plants
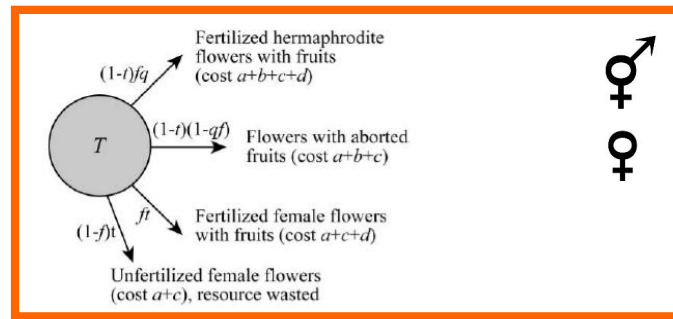


Gynomonoecious plants

# Hermaphrodite Plants



$fq$ → Fertilized flowers with fruits (cost $a+b+c+d$)

$f(1-q)$ → Fertilized flowers with aborted fruits (cost $a+b+c$)

$1-f$ → Unfertilized flowers (cost $a+b+c$)
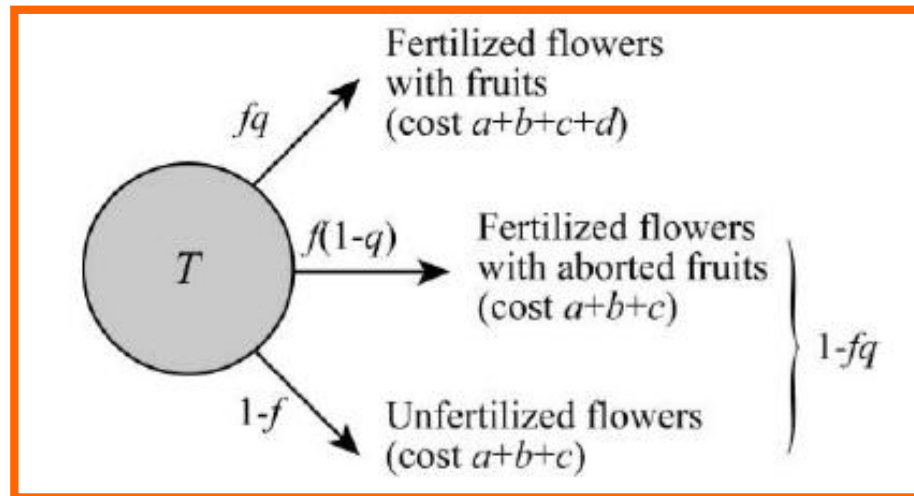
$T$

$1-fq$
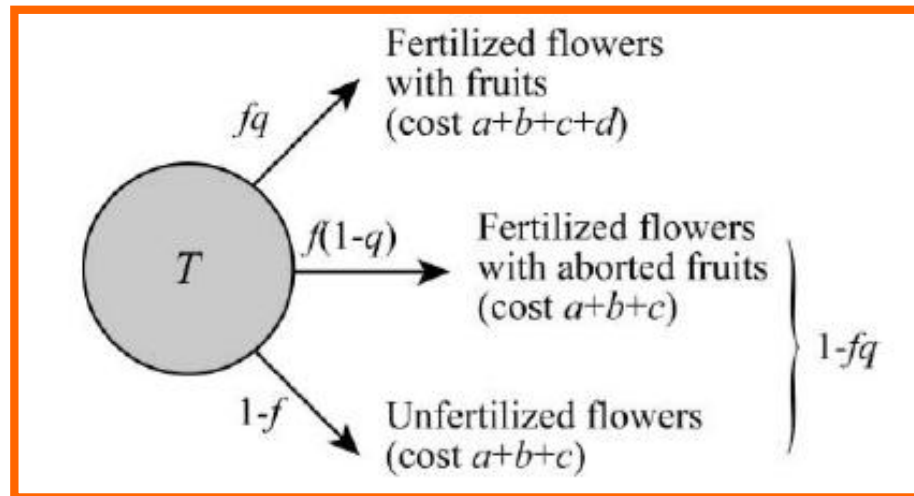
## Fitness

$$W = 2 \times \text{seeds common type}$$

$$W_m = \text{seeds mutant} + \left[ \frac{\text{pollen mutant}^a}{\text{pollen common type}^a} \right] \times \text{seeds common type}$$
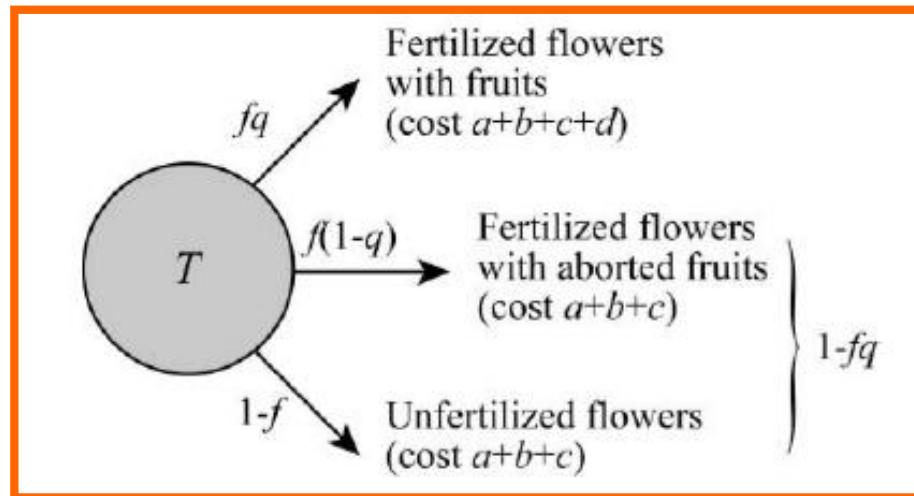
# Hermaphrodite Plants



$$W = 2qfTd/(a + b + c + d)$$

$$W_{\mathrm{m}} = \frac{q_{\mathrm{m}}fTd}{a+b+c+d} + \left[ \frac{\dfrac{q_{\mathrm{m}}fT}{a+b+c+d} + \dfrac{(1-fq_{\mathrm{m}})T}{a+b+c}}{\dfrac{qfT}{a+b+c+d} + \dfrac{(1-fq)T}{a+b+c}} \right]^{\alpha} \frac{qfTd}{a+b+c+d}$$

# Hermaphrodite Plants



Fitness maximization gives ESS $q*$

$$q* = \frac{a+b+c+d}{(\alpha+1)df} \qquad \text{if } a+b+c+d < (\alpha+1)df$$

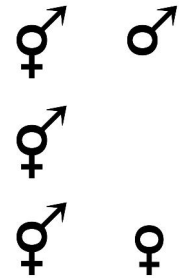$$q* = 1 \qquad \text{if } a+b+c+d \geq (\alpha+1)df$$

# Sex Systems related to Fruit Size
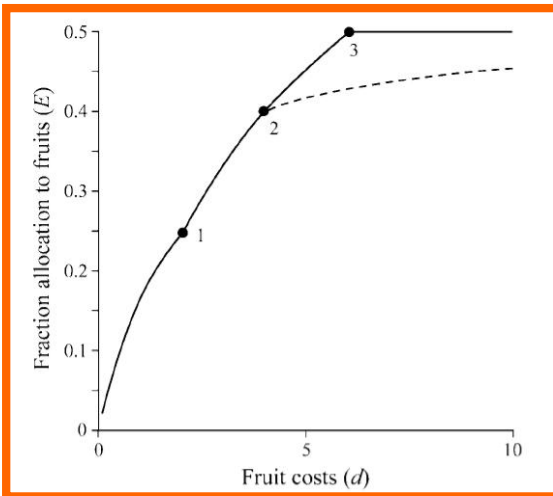


To the right of 2:  andromonoecy

Between 1 and 2:  hermaphrodite

To the left of 1:  gynomonoecy

Most likely evolutionary scenario:

a hermaphrodite ancestor makes large fruits;  mutants with some male flowers invade;  the presence of male flowers largely reduces the threshold for producing female flowers;  the system evolves to monoecy.

# Sex of Trees and Evolutionary Stable Strategies

Question addressed in the paper:

Which ecological factors favour the transition

from the hermaphrodite system to that of monoecy?

Conclusions in the paper:

When sex allocation at the flower level is strongly female-biased,

plants respond by producing either male flowers or flowers without fruits.

Hermaphroditism evolves to andromonoecy (male and hermaphrodite

flowers on the same plant) and then to monoecy (male and female

flowers on the same plant).

High costs of attraction favour producing hermaphrodite flowers.

Monoecious species are likely to have (1) small, inexpensive flowers,

(2) large, costly fruits and (3) high fertilization rates.

# Work in Progress

- Ovipositioning behavior of parasitoid wasps (with T. Keasar, M. Bügler)
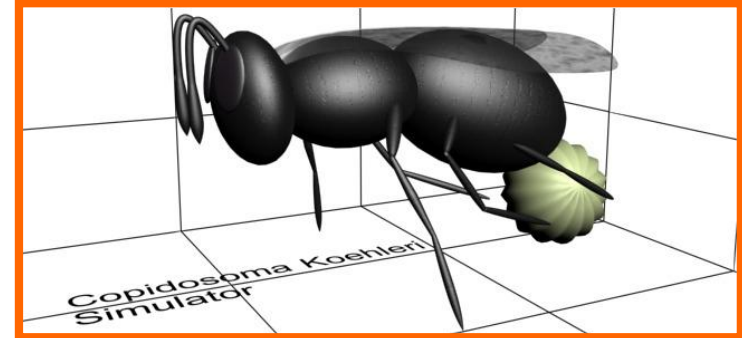


- Bird broods and cooperative games (with S. Forbes, J. Derks)



- Patch formation, local competition and evolutionary dynamics
  (with P. Uyttendaele, R. Westra, G. Schoenmakers)
- Seasonal fitness and evolutionary dynamics
  (with P. Uyttendaele, R. Westra, G. Schoenmakers)

**Maastricht University**

# Thank you for your attention!

The papers discussed are available at my homepage;
this presentation will be posted there as well.

Comments are welcome any time.

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