Handout on **Evolutionarily Stable Strategies (ESS)**
(Lecture "Evolutionary Ecology")

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Contents

1 Intro to ESS

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Some of the questions we want to answer

- Why do male lions share their harem with weaker males?

- Why do some birds kill their brothers or sisters?

- Why don't ant workers have own offspring?

- Why do vampire bats sometimes share their blood meal with starving neighbors?

- Should biologists understand mathematical modelling?

1.1 Main ideas

Nothing in Biology Makes Sense

         Except in the Light of Evolution

                  Theodosius Dobzhansky, 1973

1.2   Debate about group selection

Some popular statements

- "When two lions fight, the winner will always keep the loser alive, as killing would endanger the survival of the species"

- "Salmons swim thousands of miles from the oceans up the small rivers where they spawn. Then they die to facilitate the survival of the species."

- "When there is not enough food, all individual produce less offspring, such that the whole population can survive."

Does this make any sense at all???

Problem: If few individuals defect, they will profit from all the altruists and spread their defector alleles in the population.

Categorical Imperative

Handle nur nach derjenigen Maxime, durch die du zugleich wollen kannst, dass sie ein allgemeines Gesetz werde.

Immanuel Kant (1724-1804)

"Act only according to that maxim whereby you can at the same time will that it should become a universal law without contradiction."

Does this work in nature?

Högsted (1980) counted eggs in magpie nests in southern Sweden:

~ 5 in poor territories

~ 8 in good territories

Group selection?

Alternative explanation: the magpie lays as many eggs as she can feed as chicks, given the quality of the territory.

Högsted substantiated this with experiments in which he manipulated the number of eggs in the nests.

Arguments in the group selection debate

- What if there are many groups of individuals and there is between-group competition?

- Groups with more cooperators could be more productive.

- Is between-group selection for cooperation as fast and efficient as within-group selection for defectors?

- Simpson paradox: even if within each group defectors have higher fitness than cooperators, in total cooperators can still have higher fitness.

- But why do groups differ in frequency of cooperators? If this is caused by relatedness within groups, then this can be seen as kin selection.

- To analyze the natural fitness of all individuals may be easier for mathematical modeling than to analyze costs and indirect fitness effects of some behavioral (or other) trait.

Example: Alarm calls
Debated: do ground squirrels
bring themselves into danger
by warning the others?

- Ground squirrels warn more often when relatives are around.

- Mainly females warn. They are more often close to relatives than males.

- Sherman observed that 8% of young Belding ground squirrels were killed by male conspecifics from other clans.

selfish gene **approach:** See it from the perspective of the allele for the alternative behavior: will it become more frequent in the population?

interpretation of relatedness: if focal individual x has the very rare allele, then the probability that Y has it too, is approx. the **relatedness** from x to y.

But be cautious: but note that method of Queller and Goodnight (1989) of estimating relatedness values from genetic markers can lead to negative values, as it gives values relative to population averages

Hamilton rule
A behavior will increase the inclusive fitness of the actor if

$$\sum_i r_i \cdot B_i > C.$$

C cost, i.e. reduction of own offspring

B_i benefit, i.e. increase in offspring, for i-th beneficiary

r_i relatedness of actor to i-the beneficiary, i.e. probability the latter also has the allele for this behavior

Haldane: *I would give my live for two brothers or eight cousins.*

Wife sharing in the Tasmanian native hen
Tasmanian nativehen
sex bias: many males

Some female breeds with two males

One male is dominant but accepts the other

All three care for the offspring
Why does the dominant male accept the other?

Observed reproductive success (Maynard Smith, Ridpath, 1972)
Mean number of surviving offspring per season:

	first time	experienced
couple	1.1	5.5
trio	3.1	6.5

Total number of surviving offspring (2 to 5 seasons):

	after 2 seasons	after 5 seasons
couple $N_1 =$	6.6	23.1
trio $N_2 =$	9.6	29.1

Cost C of cooperation for dominant male: $C = N_1 - \frac{1}{2}N_2$ (Assuming each male in trio sires half of the offspring)

Cost C and benefit B of cooperation:

Cost for the dominant: $C = N_1 - \frac{1}{2}N_2$

Benefit for the accepted: $B = \frac{1}{2}N_2$.

Hamiltons rule:

$$r \cdot B > C$$

Does Hamilton's rule explain cooperation here?

$$r \cdot B - C > 0 \qquad ?$$

$r \cdot B - C =$

	after 2 seasons	after 5 seasons
If fathers unrelated $0 \cdot B - C =$	-1.8	-8.550
If fathers brothers $r \cdot B - C =$	0.6	-1.275

In fact in most trios the males are brothers.

Evolutionarily Stable Strategy (ESS)

References

[MP73]   J. Maynard Smith, G.R. Price (1973) The logic of animal conflict *Nature* **246**: 15–18

[D89]   R. Dawkins (1989) *The Selfish Gene*, 2nd edn. Oxford Paperbacks, Oxford

[DKW12] N.B. Davies, J.R. Krebs, S.A. West (2012) *An Introduction to Behavioral Ecology*, 4th edition Wiley-Blackwell, Oxford

Evolutionarily Stable Strategy (ESS)

- We don't know the ecological conditions in the past

- Therefore, it's hard to say why some strategy (behavior or other trait) could evolve

- Instead we analyze if/why the strategy is **evolutionarily stable**,

- that is, if/why other strategies cannot spread in the population under current conditions.
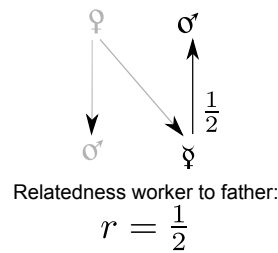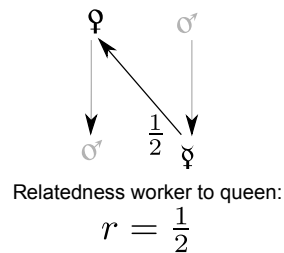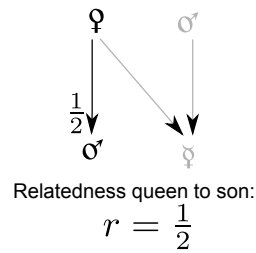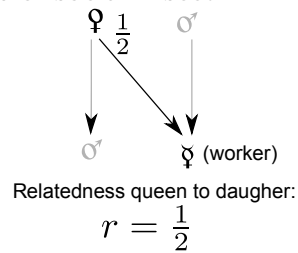
Simplifying assumptions:

- There is a single allele for the other strategy

- This allele is very rare in the population

- Thus, if unrelated individuals interact, we can neglect the possibility that both have the allele. This makes analyses much easier!

- No need for genetic realism; aim is to understand selection

Essentially, all models are wrong,

but some are useful.

G.E.P. Box

1.3 Example: Eusociality and Policing

Relatedness in nests of social insect

Relatedness queen to daugher:
$$r = \tfrac{1}{2}$$

Relatedness queen to son:
$$r = \tfrac{1}{2}$$

Relatedness worker to queen:
$$r = \tfrac{1}{2}$$

Relatedness worker to father:
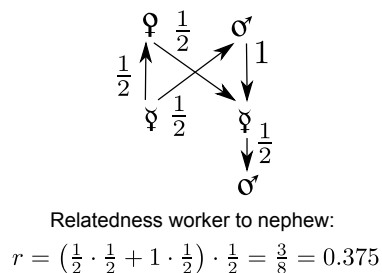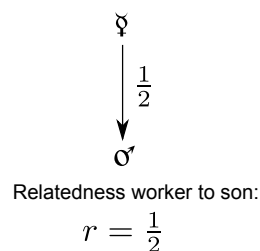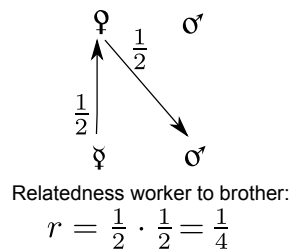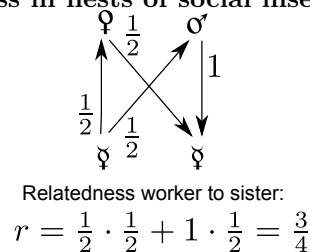$$r = \tfrac{1}{2}$$

(assuming one queen mated with one male)

Why is eusociality evolutionarily stable?

- In fact, workers can produce male offspring.
- Why is this behavior rare?
- It is observed that sons of workers are killed by the queen or other workers (*policing*).
- Thus, allele that lets workers produce more own offspring cannot increase in frequency.

Why is eusociality evolutionarily stable?

- But why this policing behavior?
- Is it evolutionarily stable?
- Would a gene in queens (or in the other workers) that impedes policing spread in the population?

More on relatedness in nests of social insect

Relatedness worker to sister:
$$r = \tfrac{1}{2} \cdot \tfrac{1}{2} + 1 \cdot \tfrac{1}{2} = \tfrac{3}{4}$$

Relatedness worker to brother:
$$r = \tfrac{1}{2} \cdot \tfrac{1}{2} = \tfrac{1}{4}$$

Relatedness worker to son:
$$r = \tfrac{1}{2}$$

Relatedness worker to nephew:
$$r = \left(\tfrac{1}{2} \cdot \tfrac{1}{2} + 1 \cdot \tfrac{1}{2}\right) \cdot \tfrac{1}{2} = \tfrac{3}{8} = 0.375$$

(assuming one queen mated with one male)

Evolutionary stability of policing by other workers?

intuitive answer: The workers are more closely related to their nephews than to their brothers, so they love their nephews much more and don't kill them.

detailed scientific answer: If one of the 3 alleles that the parents bring into to population is a no-policing allele and if this increases the number of worker sons, then more than $\frac{1}{3}$ of the males produced by the nest will have the no-policing allele. Thus, the frequency of the no-policing allele will increase.

conclusion: policing by workers is not evolutionarily stable.

Proof of detailed logical answer

Let p be the very small frequency of the no-worker-policing allele N. Then, in a fraction of $\approx 3 \cdot p$ of all nests, one of the two alleles of the queen or the father's allele is N. (You see? Here it makes things easier to assume that p is very small, as we can neglect the case that more than one of the three alleles is N)

With probability $2p$, the queen contributes allele N and half of the workers get it, and with probability p the father contributes allele N and all workers get it. Let's assume that in the first case, a fraction $a \geq 0$ and in the latter case, a fraction $b > a$ of the males produced are worker sons.

Then, among the males in the next generation, the frequency of carriers of allele N is $2p \cdot \left(a \cdot \frac{1}{2} \cdot \frac{1}{2} + (1-a) \cdot \frac{1}{2}\right) + p \cdot \left(b \cdot \frac{1}{2} + (1-b) \cdot 0\right) = p \cdot \left(1 + \frac{b-a}{2}\right) > p$ and thus has increased (details demonstrated on the black board).

Evolutionary stability of policing by the queen

intuitive answer: The queen is more closely related to her sons, so she prefers to give resources to them and no to her grandsons.

short answer: policing by the queen is evolutionarily stable.

detailed, scientific answer: Exercise for you!

What if the queen has mated with $n > 1$ males?

Then the probability of two workers to have the same father is $\frac{1}{n}$.

Relatedness worker to (half) brother:
$$\frac{1}{2} \cdot \frac{1}{2} = \frac{1}{4}$$

Relatedness worker to nephew:

$$\left(\frac{1}{2} \cdot \frac{1}{2} + \frac{1}{2} \cdot \frac{1}{n} \cdot 1\right) \cdot \frac{1}{2} \; < \; \frac{1}{4} \qquad \text{if} \quad n > 2$$

Thus, worker policing can be evolutionarily stable if the queen is usually multiply mated.
In honey bees, queens are usually multiply mated.
Ratnieks and Visscher (1989) report that honey bee
workers destroy the eggs of other workers and take
care for eggs layed by the queen.

Wenseleers and Ratnieks (2006) compared 48 species of ants, bees, and wasps. They found that worker policing is indeed more common in species where queens mate more frequently.

References

[1] F.L.W. Ratnieks, P.W. Visscher (1989) Worker policing in the honeybee *Nature* **342**: 796–797

[2] T. Wenseleers, F.L.W. Ratnieks (2006) Comparative analysis of worker reproduction and policing in eusocial hymenoptera supports relatedness theory. *American Naturalist* **168** E163–E179

1.4   Example: Siblicide in Birds

Nazca Booby (*Sula granti*)
- Mother usually lays two eggs

- When the first offspring hatches, it throws the other egg out of the nest.

- Is this evolutionarily stable?

References

[1] D.J. Anderson (1990) Evolution of Obligate Siblicide in Boobies 2: Food Limitation and Parent-Offspring Conflict. *Evolution* **44.8**: 2069–2082

[2] C.A. Humphries, V.D. Arevalo, K.N. Fischer, D.J. Anderson (2006) Contributions of marginal offspring to reproductive success of Nazca booby (Sula granti) parents: tests of multiple hypotheses. *Oecologica* **147.2**: 379–390

Nazca Booby (*Sula granti*)

First the simple question: Why do parents lay two eggs if one will be destroyed anyways?

Answer: To have a back-up egg if the first one fails.

Could a killer allele K spread in the population?

Idea: First hatching offspring ("Caine") gets more food and has better chance to survive if it kills its sibling ("Abel").

Simple model:

K dominant allele if in Caine will make it kill Abel.

ℓ peaceful allele, recessive

p frequency of K

First consider the case that p is very small $\Rightarrow$ neglect KK genotype.

Genotype	Survival probability	
Caine	Caine	Abel
$\ell\ell$	c	a
$K\ell$	$c + m$	$a - d$

Frequency of families with one $K\ell$ parent and one $\ell\ell$ parent:

$$2 \cdot p \cdot (1 - p) \cdot (1 - p)^2 \cdot 2 \quad \approx \quad 4p$$

How many $K\ell$ will such a couple produce? (We assume that if Caine is $\ell\ell$ and Abel is $K\ell$, then Abel will kill Caine and has benefit m)

Probability	Caine	Abel	$K\ell$ offspring
$\frac{1}{4}$	$\ell\ell$	$\ell\ell$	0
$\frac{1}{4}$	$\ell\ell$	$K\ell$	$a + m$
$\frac{1}{4}$	$K\ell$	$\ell\ell$	$c + m$
$\frac{1}{4}$	$K\ell$	$K\ell$	$c + m + a - d$

To calculate the allele frequencies in the offspring produced in a season we need to relate the fraction of families with K allele and their productivity to the productivity of the families without K allele:

$$\frac{4p \cdot \frac{1}{4}(a + m + c + m + c + m + a - d)}{(a + c)} \cdot \frac{1}{2} \quad = \quad p \cdot \left(1 + \frac{3m - d}{2 \cdot (a + c)}\right)$$

Conclusion: the K allele can spread if $3m > d$, that is, if the Caine's benefit of killing is more than three times as high as the cost of Abel's death (in terms of probability of surviving until sexual maturity).

This is in contrast to empirical observations:

- Nowadays all nazca boobies are killers!

- $a - d = 0$

- Researchers prevented killing and found that both offspring have a good chance to survive. They estimated:

  - $c + d = c + a > 0.9$
  - $c + m = 0.6$
  - Assuming $c \geq a$ implies $c \geq 0.45$, $m \leq 0.15$ and $d - m > 0.3$
  - Thus, $d - 3m > 0$, which contradicts $3m > d$.

Conclusion: Under present day conditions, the **absence** of siblicide would be evolutionarily stable.

Perhaps conditions were different in the past. We should better ask for for evolutionary stability of siblicide under present conditions.

Now assume:

L rare dominant allele that prevents killing when in Caine

k recessive allele for killing

Most parents are kk×kk and have $(c + m)/2$ offspring per kk parent.

If one parent is Lk, we assume that Lk Caine can survive only if Abel is also Lk.

Probability	Caine	Abel	Lk offspring
$\frac{1}{4}$	kk	kk	0
$\frac{1}{4}$	kk	Lk	0
$\frac{1}{4}$	Lk	kk	0
$\frac{1}{4}$	Lk	Lk	$c + a$

Thus, per Lk parent there are $(c + a)/4$ Lk offspring, which is less than $(c + m)/2$ as $c \geq a$.

Conclusion: This model may explain why siblicide still takes place and is evolutionarily stable.

First General Conclusions

- Simple mathematical models help to assess whether some qualitative explanation...

  - ...does make sense at all and
  - ...is in accordance with empirical data.

- One can start with a very simple model (e.g. only one dominant allele) and later discuss whether the conclusions will be different if the model is refined.

1.5 Example: Siblicide in Wasps

In many species of parasitoid wasps

- mother lays several eggs into the host

- larvae kill each other

- only one larva survives per host

See Godfray (1987) for detailed mathematical analysis and e.g. Mayhew et al. for references on empirical studies.

If there is one larva with siblicide gene, there is selection pressure for others to have it too.

If siblicide gene is in the population, there is selection pressure for small brood sizes.

Even then, laying "insurance eggs" may be advantageous.

If mothers lay only one egg, siblicide allele can vanish, giving fitness advantage of laying more eggs.

Even for larger brood sizes non-siblicide allele can have higher inclusive fitness if siblings are closely related due to inbreeding.

References

[PM87] G.A. Parker, D.W. Mock (1987) Parent-offspring conflict over clutch size *Evolutionary Ecology* **1**: 161–174

[G87] H.C.J. Godfray (1987) The evolution of clutch size in parasitic wasps *The American Naturalist* **129**: 221–233

[MO+98] P.J. Mayhew, P.J. Ode, I.C.W. Hardy, J.A. Rosenheim (1998) Parasitoid clutch size and irreversible evolution *Ecology Letters* **1**: 139–141

2 Game Theory in Behavioral Ecology

2.1 Reciprocity

Mutualism: Cooperative behavior of two or more individuals in which all indiviuals increase their expected number of offspring.

e.g. group of male lions sharing a harem that a single lion could not defend.
Reciprocity, reciprocal altruism: Mutualism in which the return service comes later.

- Why will the first beneficiary really pay back?
- Why does the first trust the beneficiary?

2.2 Example: Altruistic Vampire Bats

Altruistic vampire bats

Observed behavior:

1. vampire found host and had a blood meal,

2. returns to home cave,

3. regurgitates blood and feeds starving (unrelated) neighbors

Explanation: they trust that the others may, in return, save them from starvation at some later occasion.
But why couldn't a free-rider strategy spread in the population?

2.3   Prisoners' Dilemma and Tit For Tat

Prisoners' dilemma

- Two prisoners A and B have been involved in the same two crimes.

- Based on evidence for the first crime, each of them is sentenced to one year of prison.

- The judge offers each of them a deal:

    - If A testifies that B comitted the 2$^{\text{nd}}$ crime, A is set free and B gets 3 years.
    - If B testifies that A comitted the 2$^{\text{nd}}$ crime, B is set free and A gets 3 years.
    - If A and B testify against each other, both stay 2 years in prison.

What will happen if each of the prisoners tries to minimize his imprisonment?

Before we get depressed, let's reformulate this as a game:

Each played can either cooperate with the other player or defect, and the payoff for player A will depend on her strategy and that of player B.

payoff matrix for player A:

		player B	
		cooperate	defect
player A	cooperate	R=0	S=-2
	defect	T=1	P=-1

R = reward S = sucker's payoff

T = temptation P = punishment

In prisoners' dilemma:

$$S < P < R < T$$

In the prisoners' dilemma, it is always better for A to defect, no matter what B does. And vice versa. If both play rationally, they will both defect and get less payoff (stay longer in prison) than if they cooperate with each other.

- So far, we have assumed that the players meet only once.

- If the play several times, they can create confidence in each other by always cooperating and obtaining a payoff of 1 in each game.

- In many players are involved that meet randomly: The more players cooperate, the higher is the payoff of defecting.

- R. Axelrod performed computer simulations of individuals that interacted with 62 different strategies. Quite successful was **Tit for Tat**.

References

[AH81] R. Axelrod, W.D. Hamilton (1981) The evolution of cooperation. *Science* **211**: 1390–1396

[A84] R. Axelrod (1984) *The Evolution of Cooperation.* Basic Books, New York

The strategy Tit for Tat

- If you meet some player X the first time, cooperate

- If you meet a player X that you have met before, do what X did last time.

If two individuals meet, let q be the propability that they will meet again some time. If both play tit for tat, the expected total payoff of each player is:

$$R + q \cdot (R + q \cdot (R + \cdots)) \;=\; R + q \cdot R + q^2 \cdot R + q^3 \cdot R + \cdots \;=\; \frac{R}{1-q}$$

What is the total payoff of player A if

- A always defects, and

- interacts with player X whose strategy is tit for tat?

$$T + qP + q^2 P + q^3 P + \ldots = T + \frac{q \cdot P}{1-q}$$

And what is A's payoff if A first defects, then cooperates, then defects, then cooperates, and so forth?

$$T + q \cdot S + q^2 \cdot T + q^3 \cdot S + \cdots \;=\; \frac{T + q \cdot S}{1 - q^2}$$

If the players are individuals of a population and the payoffs are offspring numbers, **Tit for Tat** can only be an **Evolutionarily Stable Strategy**, if it is stable against the previous two strategies, that is if the following two conditions hold:

$$\frac{R}{1-q} \;>\; T + \frac{q \cdot P}{1-q}$$
$$\frac{R}{1-q} \;>\; \frac{T + q \cdot S}{1 - q^2}$$

Or, equivalently, the probability q to meet again must be larger than

$$\frac{T-R}{T-P} \quad \text{and} \quad \frac{T-R}{R-S}.$$

2.4   The return of the vampires

G. Wilkinson marked and observed many vampire bats in Costa Rica

- Bats feed relatives and other bats that were constant companions in the roosts

- Also non-related individuals share a roost for years. Thus, q is large.

- Only bats who urgently need food are fed.

- Vampires who had no blood meal for a while will die. Thus, $R - S$ is large.

References

[W84] G.S. Wilkinson (1984) Reciprocal food sharing in the vampire bat. *Nature* **308**: 181–184

2.5 Other examples for Tit For Tat

Mating behavior of the black hamlet
The black hamlet (*Hypoplectrus nigricans*) is a simultaneous hermaphrodite.

Mating behavior:
A lays eggs,
B inseminates eggs,
B lays eggs,
A inseminates eggs,
A lays eggs,
B inseminats eggs,
$\vdots$
Eggs are more costly than sperm. If one stops laying eggs, the other will leave.

Grooming in monkeys
Observation: unrelated monkeys who groom each other will also help each other in dangerous situations.

Tit for tat?

2.6 Other games and optimal strategies

Nash equilibrium
A game with n players is in **Nash equilibrium**, if no player can improve her payoff by changing (only) her strategy.

Theorem 1 (Nash's existence theorem) *For each game with n players in which each player is allowed to mix finitely many elementary strategies (that is, define probabilities for the strategies and choose a random elementary strategy for the game) there is at least one Nash equilibrium.*

References

[N50] J. Nash (1950) Equilibrium points in n-person games *PNAS* **36(1)**:48–49.

For these few lines in PNAS, see `http://www.pnas.org/content/36/1/48.full.pdf+html`, John Nash obtained the 1994 Nobel Prize in Economy (along with John Harsanyi and Reinhard Selten).

Paper, Scissors, Stone
Simple example: if you play "Paper, Scissors, Stone" every deterministic strategy will always be beaten by another strategy. The mixed strategy to always choose any of paper, scissors, and stone with probability $\frac{1}{3}$ will win in half of the cases.

3 Conclusion

Conclusion

You as a biologist must learn to understand mathematical formulas, models and analyses because you need this

- to understand the literature,

- to make your ideas about a biological process precise,

- to check whether your ideas make sense at all,

- to check whether your ideas are supported by empirical data.