Evolutionarily Stable Strategies (ESS)

1) The ESS approach

2) Frequency-dependent selection

3) The Hawk-Dove game

4) Sex ratio as an ESS

5) Alternative reproductive phenotypes

6) Conditional strategies

7) Tit-for-tat and the evolution of cooperation

8) Example exam questions

1) The ESS approach

A body of ideas developed to help understand evolutionary processes when natural selection is frequency-dependent. Selection is rarely measured, but theory is used to predict phenotypes at equilibrium.

Some jargon (derived from game theory in mathematics):

strategy: a program of action; a phenotype;
(term doesn't imply goal-directed behavior when applied to nature)

tactic: exercising the program in a particular situation

payoff: fitness

Approach assumes that:
The underlying genetics is the simplest possible;
That payoffs reflect the number of offspring for each allele;
Enough mutation occurs to allow each strategy the opportunity to invade.

Grafen (1991) called this the 'phenotypic gambit'.

1) The ESS approach

Definition of ESS:

A single strategy is an ESS if, when it is adopted by most members of the population, it cannot be supplanted by a mutant (rare) playing an alternate strategy.

John Maynard Smith was a major contributor to development of this approach in the study of behavior and evolution (also Fisher, Parker, Hamilton and MacArthur before him).

Web of Stories.
Wikimedia Commons - http://commons.wikimedia.org/wiki/File:John_Maynard_Smith.jpg#mediaviewer/File:John_Maynard_Smith.jpg

2) Frequency-dependent selection

The “payoff” (fitness) of each “strategy” (phenotype) depends on its frequency in the population.

Example: In *Heliconius* butterflies, 100% postman is an ESS. So is 100% rayed. When either form is most common, the other form cannot invade when rare.

http://en.wikipedia.org/wiki/File:Heliconius_mimicry.png

3) The Hawk-dove game

Invented to help develop our understanding of the evolution of aggression in wild populations

When played against

Fitness of		H	D
	H		
	D		

Two strategies in the game, Hawk and Dove;

Hawk: fight to win, retreat only if injured
Dove: Posture only. Retreat if opponent escalates.

3) The Hawk-dove game

Payoff matrix

When played against

Fitness of		H	D
	H		V
	D	0	

From Rose, M.R. and L.D. Mueller. 2006. Evolution and Ecology of the Organism. Pearson Prentice Hall.

3) The Hawk-dove game

When played against

Fitness of

	H	D
H		V
D	0	V / 2

3) The Hawk-dove game

When played against

Fitness of		H	D
	H	(V - W) / 2	V
	D	0	V / 2

3) The Hawk-dove game

Can lead to a ***mixed*** **ESS:**
a polymorphism at equilibrium in which all strategies have equal fitness

Example case: V = 50 and W = 100

When played against

Fitness of	H	D
H	-25	50
D	0	25

Lessons from thought experiment: Aggression has costs as well as benefits; natural selection does not necessarily lead to the evolution of pure aggression; no need to appeal to 'the good of the species' to explain dove-ishness in nature.

Mixed ESS

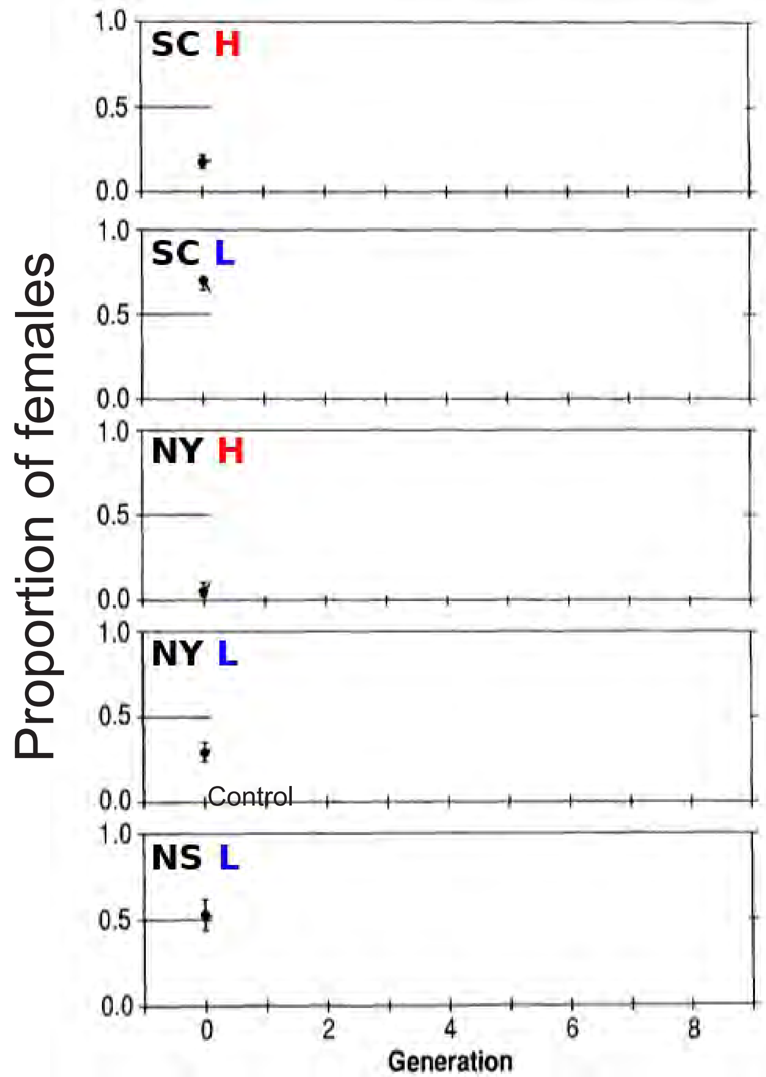
A single strategy is an ESS if, when it is adopted by most members of the population, it cannot be supplanted by a mutant (rare) playing an alternate strategy

A more complex possibility is a mixed ESS, in which either of two strategies can invade when rare. At equilibrium frequency, the population is polymorphic and both strategies have equal fitness. At equilibrium, neither strategy has a fitness benefit.

4) Sex ratio as a mixed ESS

The Atlantic silverside has temperature-dependent sex determination

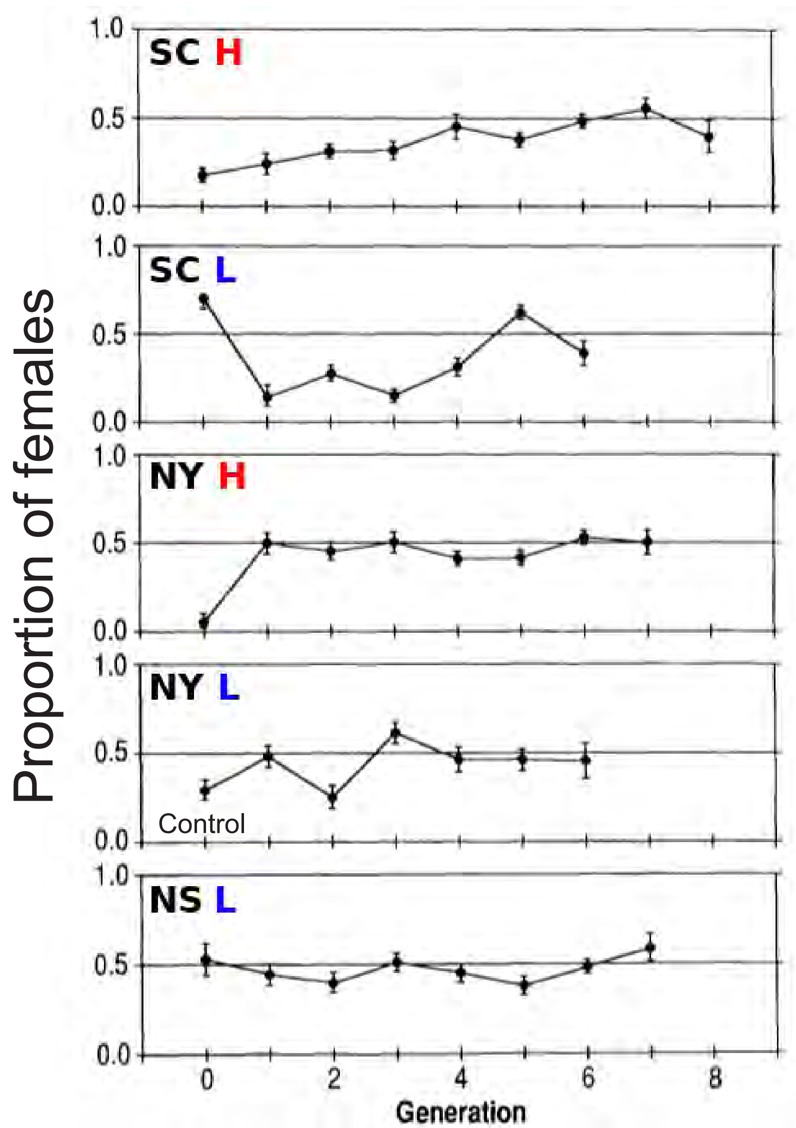
http://filaman.ifm-geomar.de/Photos/PicturesSummary.php?ID=339&what=species



Conover & Van Voorhees (1990)

4) Sex ratio as a mixed ESS

But the temperature threshold at which males or females are produced can evolve.



Conover & Van Voorhees (1990)

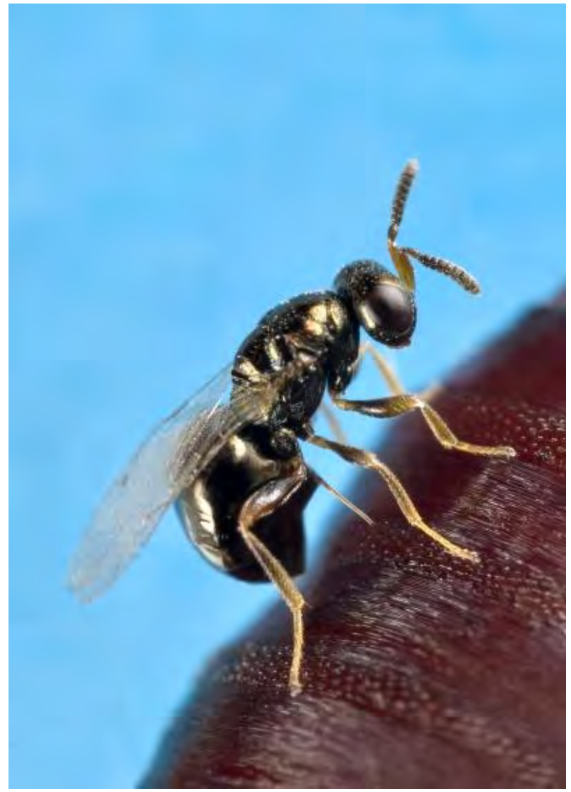
4) Sex ratio as a mixed ESS

When is a roughly 50:50 sex ratio not observed?

1) Cytoplasmic factors (e.g., *Wolbachia*)

2) Spatial structure (e.g., Nasonia)

3) Sex-specific life histories (e.g., Seychelles warbler)



http://www.eurekalert.org/multimedia/pub/19443.php?from=151980

4) Sex ratio as a mixed ESS

Nasonia vitripennis life cycle

Young wasps emerge and mate on the pupa <u>before</u> flying off. Males are flightless.

© Peter Koomen

Females fly off and lay brood of eggs in a fresh fly pupa

Larval wasps devour fly, grow big, pupate

http://www.spektrum.de/alias/interview/gene-lesen-ist-erst-die-halbe-miete/1021808
https://www.wageningenur.nl/en/show/Bart-Pannebakker-The-evolution-of-reproductive-modes-in-parasitoid-wasps.htm

4) Sex ratio as a mixed ESS

When only one female lays eggs on a single host pupa

She lays more many daughters then sons

♀♀♀♀♀♀♀♀

♂♂

When multiple females lay eggs on a single host pupa

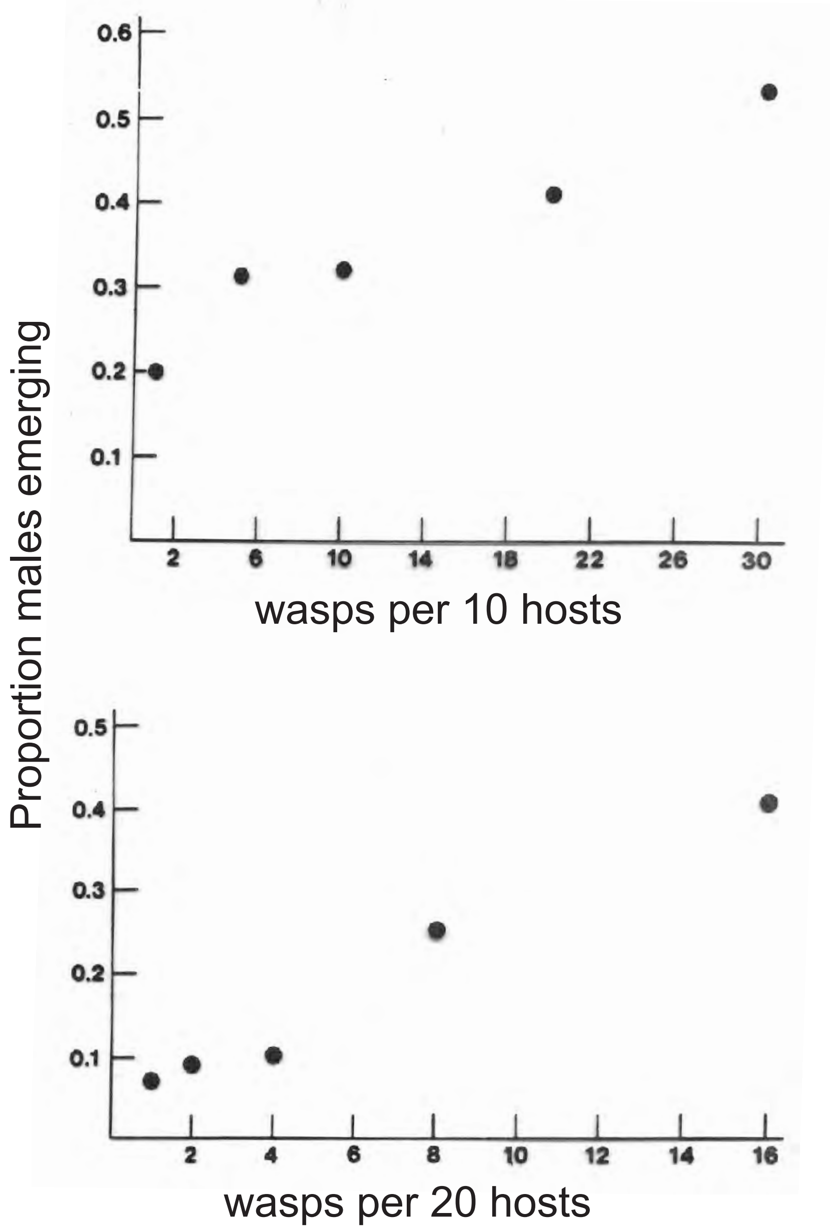
Sex ratio of their offspring is closer to 50:50

♀♀♀♀♀♀

♂♂♂♂

The leading hypothesis to explain this phenomenon is local mate competition (LMC). When mating takes place locally, brothers compete for females. This reduces the fitness benefits to females from producing male offspring.

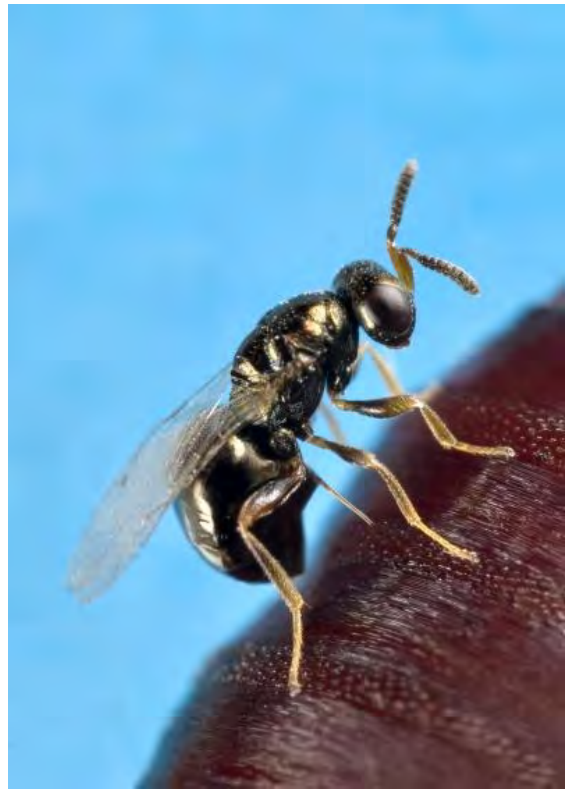
4) Sex ratio as a mixed ESS



Wylie (1965)

Velthuis et al (1965)

FIGURE 5.4. Sex ratio as a function of number of associated ovipositing females for the wasp *Nasonia* attacking fly pupae. Experimental details (e.g., blowfly versus housefly hosts, container size, etc.) varied widely among workers, yet the results are quite comparable. As predicted by LMC, sex ratio rises from few males to near equality. Walker's 1967 data show a clear asymptote.



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Sex ratio adjustment in the Seychelles warbler

Hypothesis: female offspring remain on territory and help parents raise next broods. This is a net benefit to parents when territory quality is high but not when quality is low because of greater competition for food.

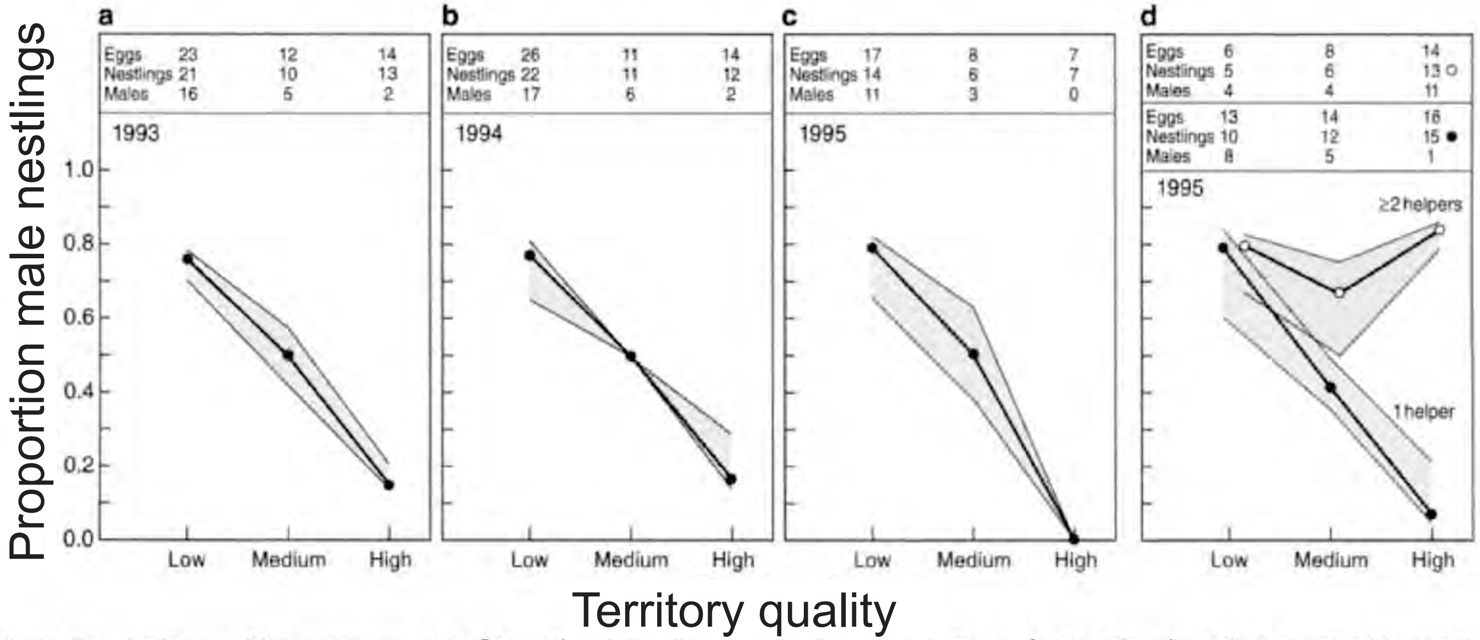


Figure 1 Sex ratio in Seychelles warbler nestlings. **a**–**c**, Sex ratio of nestlings produced by Seychelles warbler pairs in relation to quality class of breeding territory (*tq* classes: 1, low-quality territory; 2, medium-quality territory; and 3, high-quality territory; 1993–1995). No additional young were present on the territory. Young were hatched from one-egg clutches only in different years (**a**, 1993; $n = 46$, G-test of independence: $D = 12.23$, d.f. $= 1$, $P = 0.0005$, proportion male $= 1/(1 + e^{-z})$, $z = -2.68 + 1.36(tq\ \text{class})$; **b**, 1994: $n = 45$, $D = 12.03$, d.f. $= 1$, $P = 0.0005$, $z = -2.68 + 1.37\ (tq\ \text{class})$; **c**, 1995: $n = 27$, $D = 12.99$, d.f. $= 1$, $P = 0.0003$, $z = -3.60 + 2.10(tq\ \text{class})$). If in the analysis only young were included that had been hatched from different breeding pairs and different mothers, the pattern of sex ratio of nestlings in relation to territory quality class remained the same (1993: $n = 44$, $D = 12.71$, d.f. $= 1$, $P = 0.0005$; 1994: $n = 34$, $D = 11.71$, d.f. $= 1$, $P = 0.0006$; 1995: $n = 27$, $D = 12.99$, d.f. $= 1$, $P = 0.0003$). **d**, Sex ratio of nestlings produced by Seychelles warbler pairs in relation to quality of breeding territory and to the number of helpers present (1995). ($D(tq\ \text{class}) = 13.26$, d.f. $= 1$, $P = 0.0003$; $D(\text{helper}) = 10.86$, d.f. $= 1$, $P = 0.001$; $D(tq\ \text{class} \times \text{helper}) = 11.77$, d.f. $= 1$, $P = 0.0006$; $z = -4.77 + 3.09(tq\ \text{class}) + 1.93(\text{helper}) - 1.59(tq\ \text{class} \times \text{helper})$). Shaded area represents the maximal and minimal values for the sex ratio assuming that all eggs hatched were male, or females, respectively.

Komdeur et al (1997) Nature

5) Alternative reproductive phenotypes

Species	Alternative phenotypes	Genetic polymorphism	Refs
Caloglyphus berlesei (mite)	Fight/non-fight	N	25,49
Onthophagus sp. (dung beetle)	Fight/sneak	N	15–17
Leistotrophus versicolor (rove beetle)	Dominant/female mimic	N	20
Perdita portalis (bee)	Wingless fighter/ winged non-fighter	N	18
Paracerceis sculpta (isopod)	Fight/mimic/sneak	Y	8
Limulus polyphemus (horseshoe crab)	Pair/satellite	N	21
Poecilia reticulata (guppy)	Court/sneak	N	26,27
Xiphiphorus nigrensis (swordtail)	Court/court and sneak/ sneak	Y	9–11
Porichthys notatus (midshipman)	Call/sneak	N(?)	33,38,39
Urosaurus ornatus (tree lizard)	Territorial/ranger	Y(?)	31,48
Bucephala islandica (goldeneye duck)	Nest/nest and parasitize	N	22
Philomachus pugnax (ruff)	Territorial/satellite	Y	12,13
Ficedula hypoleuca (pied flycatcher)	Monogamous/polygynous	N	19
Various rodents	Dominant/subordinate	N	36

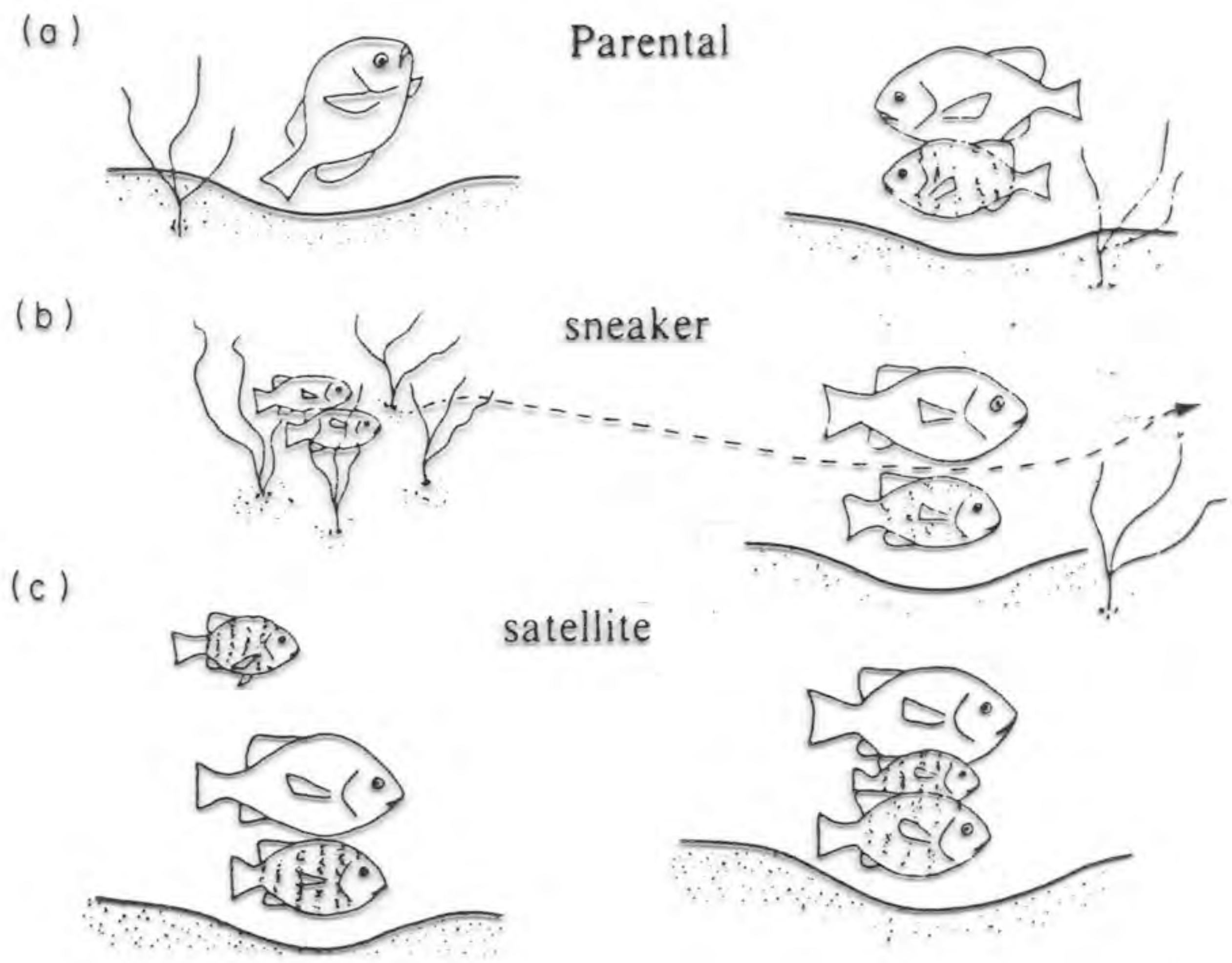
[a]Examples mentioned in the text are listed. They include most known cases with evidence for genetic polymorphism, but only a small fraction of the known cases without. Many of these papers give additional references.
[b]N, no; Y, yes; ?, unsure.

Gross (1996) TREE

5) Alternative reproductive phenotypes

Polymorphism in bluegill sunfish

Fig. 4. Schematic representation of male mating behaviour in bluegill sunfish (*Lepomis macrochirus*).

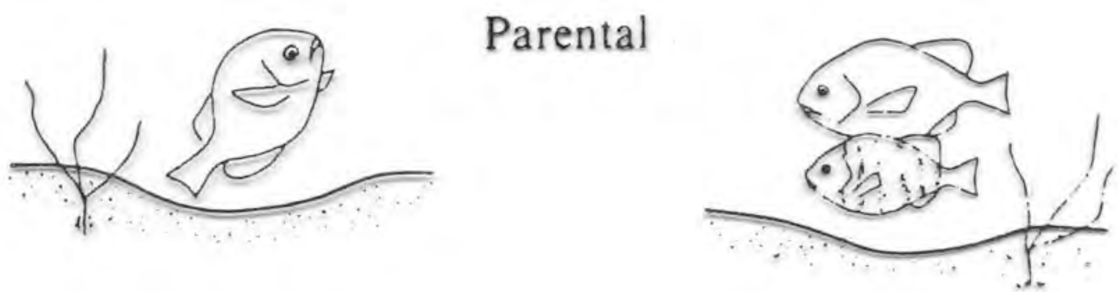


http://en.wikipedia.org/wiki/Bluegill

5) Alternative reproductive phenotypes

Parental morph

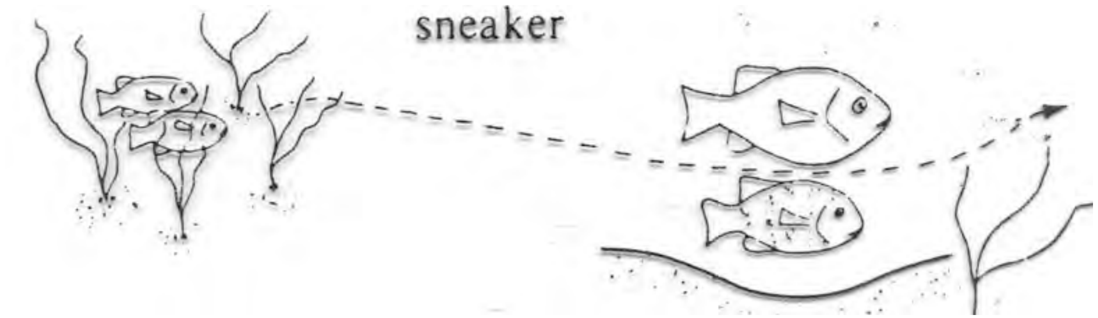
Male builds nest, attracts females
Remains at nest after spawning
Exhibits paternal care
Aggressive, large
Yellow-orange breast.



5) Alternative reproductive phenotypes

Sneaker morph

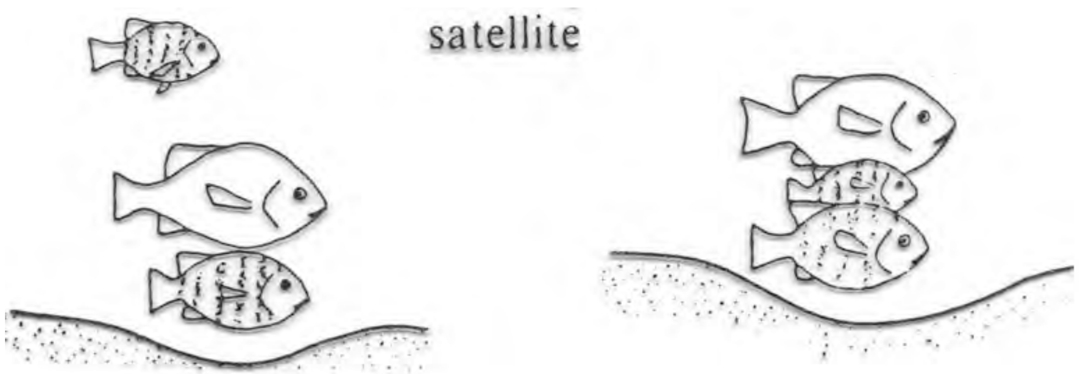
Hides near nest of parental male
Darts in during spawning, releases sperm
In Lake Opinicon, fertilizes an average of 89% of eggs in the 8% of spawning events in which they participate
Small, no breast color



5) Alternative reproductive phenotypes

Satellite morph

Hovers above the parental male and spawning female
Slowly descends next to (often between) the parental male and female, mimicking female behavior but releasing sperm
Mimics a female in color and behavior



5) Alternative reproductive phenotypes

Is it a mixed ESS? Not known.

Two basic strategies:
Parental and cuckold (sneakers and satellites)
Sneakers develop into satellites with age
But neither parental nor cuckold morph develops into the other.

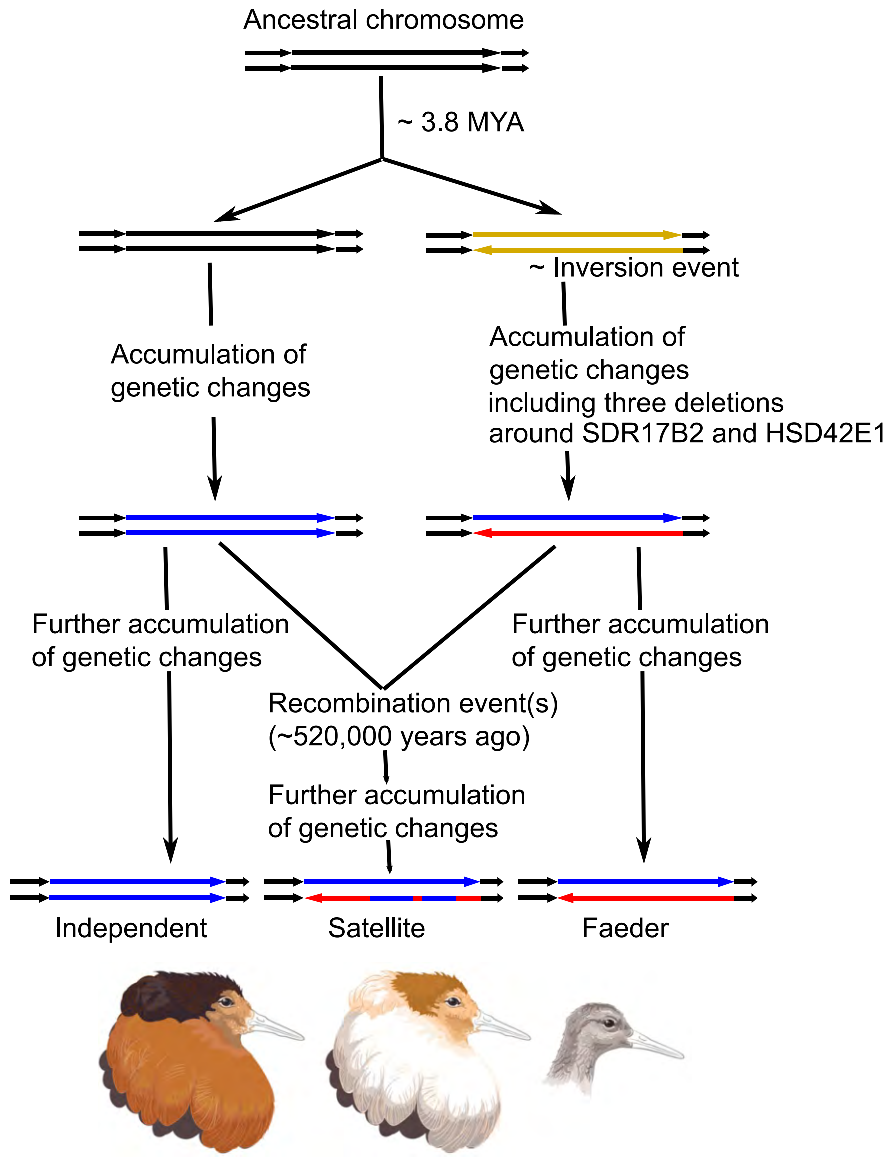
Relative numbers in Lake Opinicon:

64% sneakers } 85% !!
21% satellites }
15% parental males

5) Alternative reproductive phenotypes

Do we need to know the genes?

A supergene underlies the male polymorphism in ruff. The inversion breakpoint disrupts a gene, with the result that individuals homozygous for the inversion die. This has a strong effect on the ESS.



Lamichhaney et al. (2016) Nature Genetics; Taylor & Campagna (2016) Science

6) Conditional strategies

Alternative male reproductive phenotypes in natterjack toad

Apparently not a mixed ESS – *conditional strategy* instead

www.ecologyservices.org/images/DANoothSB0051.jpg

	Average frequency	Observed matings
Callers	67%	80.5%
Satellites	33%	19.5%

Arak (1988) Animal Behaviour

7) Tit for tat and the evolution of cooperation

[intentionally left blank]

8) Example exam questions

Give the definition of an evolutionarily stable strategy and provide an example.

Provide an example of frequency dependent selection.

How might you test whether frequency-dependent selection is occurring on a polymorphic populations?

Why might we expect natural selection to result in an equal sex ratio (1:1 for sons:daughters) in a randomly-mating, diploid populations?

Under what circumstances might natural selection favor a sex ratio that is biased in favor of females? Explain.

A marine population of cuttlefish has two male reproductive morphs, “territorial” and “female mimic,” occurring at frequency 60% and 40% respectively. Design an experiment to test whether the observed frequencies represent a mixed ESS.

How might the underlying genetic basis of an ESS affect the equilibrium frequencies of alternative morphs?