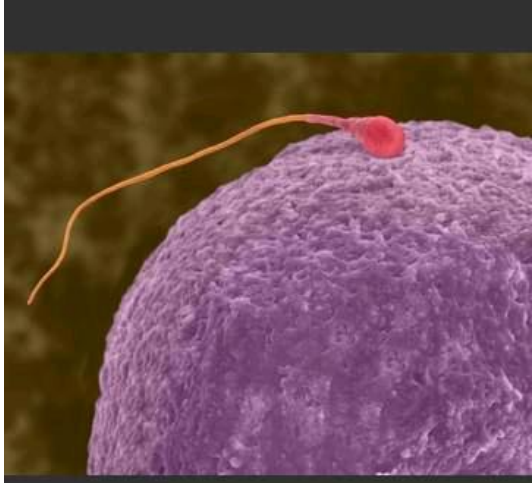
Theories for the evolution of the sexes

Priya Iyer

Evolution of Complex Systems
January 14, 2010



Outline

- Historical development of the theory
- Need for refocus, new approaches
- Models for origin of the sexes
- Evolution of ornamentation and sexual dimorphism
- New tools to study evolution of social systems

- Evolution by natural selection (Darwin, 1859)
- Theory of sexual selection (Darwin, 1871)
  - Evolution of costly, showy traits

Universal templates for male and female

"Males of almost all animals have stronger passions than females."

"The female... with the rarest of exceptions is less eager than the male... she is coy."

Females choose mates who are "more attractive... vigorous and well-armed'' just as "man can give beauty... to his male poultry."

Bateman's principle (1948)

- Female fertility limited by number of eggs produced
- Male fertility limited by the number of inseminations
- "Undiscriminating eagerness in males and discriminative passiveness in females"

Theory of parental investment

Trivers (1972)

- Amplification of differences in parental investment
- Differences in gamete sizes leads to the ‘male’ and ‘female’ strategies

Today's Central Narrative

"We now understand…

Males, who can produce many offspring with only minimal investment, spread their genes most effectively by mating promiscuously…

Female reproductive output is far more constrained by the metabolic costs of producing eggs or offspring, and thus a female's interests are served more by mate quality than by mate quantity."

(Coyne, 2004)

Conflict between the sexes

"Conflict exists because there are two sexes and therefore will be present in all anisogamous species, and has neither an evolutionary starting point nor an end"

- Arnqvist and Rowe, 2005

Conflict between the sexes

Even the origin of the sexes based in conflict

Sperm parasitizing on the investment by eggs
(Parker, Baker and Smith, 1972)

Female choice

- Direct benefits
  - Resources, male care, protection
- Good genes
  - Compatibility
  - Weeding out bad genes; hierarchy of genetic quality

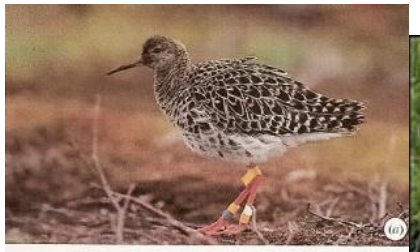
Empirical evidence

- Nearly-universal binary only in gamete sizes
- Many species hermaphroditic

Empirical evidence

- Sex changes, crisscrossing species

Multiple morphs among each sex

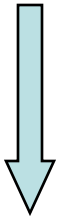


Deviations from the sex specific templates

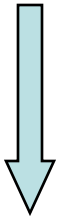
Male-only or male-biased parental care

Possible direction of evolutionary transitions in fish and birds

No parental care



Male-only parental care



Biparental care

Sex role reversal in…

- Eagerness to mate
- Dominance

Coordination between sexes in parental care, compensation for low activity levels

Same sex sexuality documented in over 300 vertebrates

Sexual interactions are social interactions

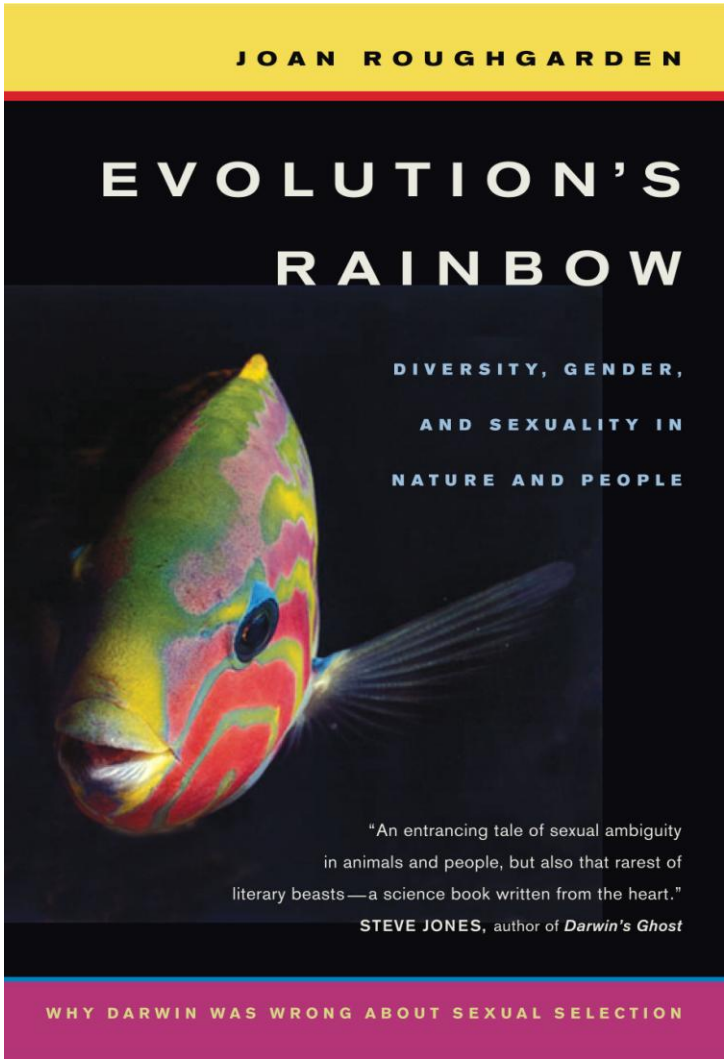
Problems with the good genes models

- Theoretical: paradox of the lek

- Lack of evidence for consistent female choice, heritable variation in fitness, correlation between sexually selected trait and fitness

Social selection program

- Questioning the primacy of conflict, sex-specific templates
- Developing alternative hypotheses for the evolution of sexual systems
- Emphasis on the social dynamics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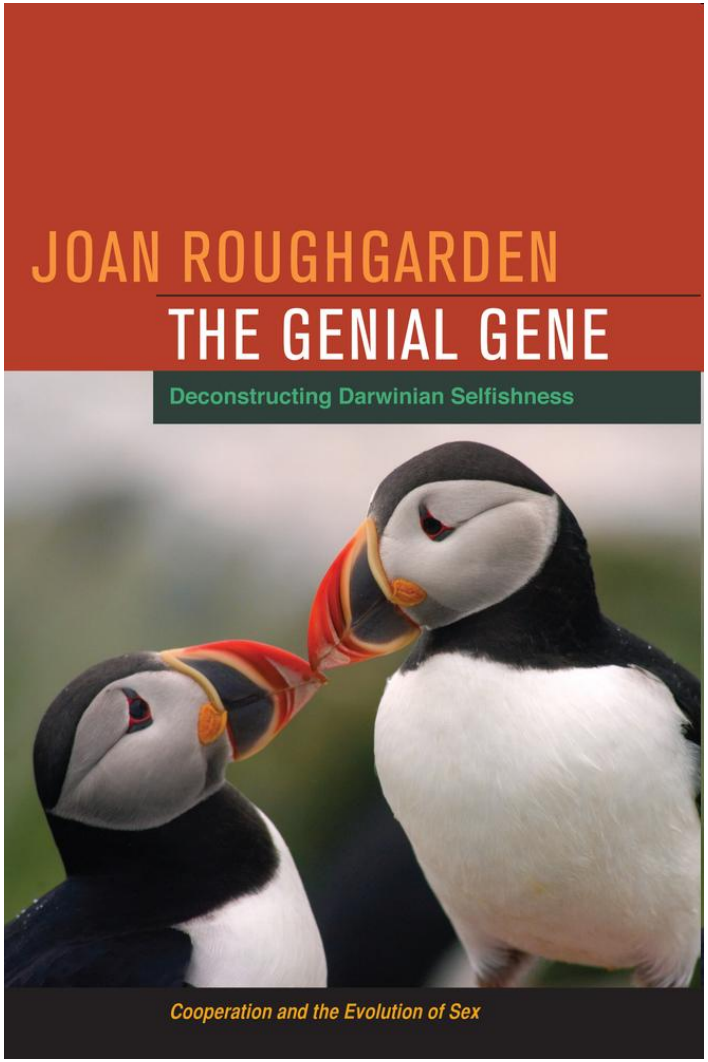
EVOLUTION'S RAINBOW
DIVERSITY, GENDER, AND SEXUALITY IN NATURE AND PEOPLE
"An entrancing tale of sexual ambiguity in animals and people, but also that rarest of literary beasts—a science book written from the heart."
STEVE JONES, author of Darwin's Ghost
WHY DARWIN WAS WRONG ABOUT SEXUAL SELECTION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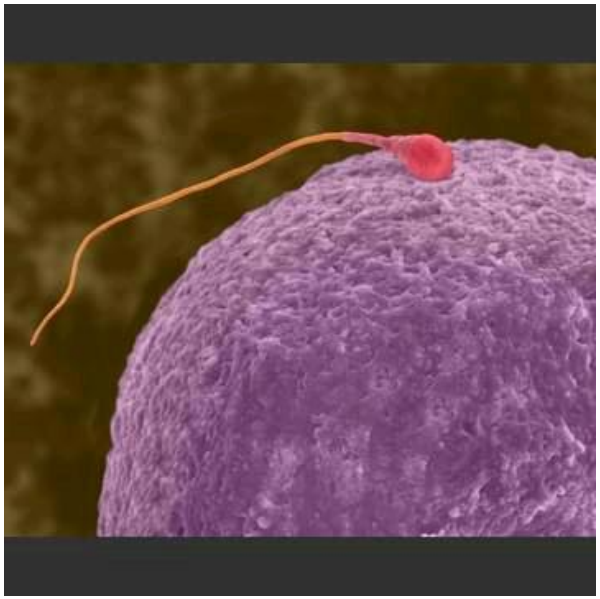
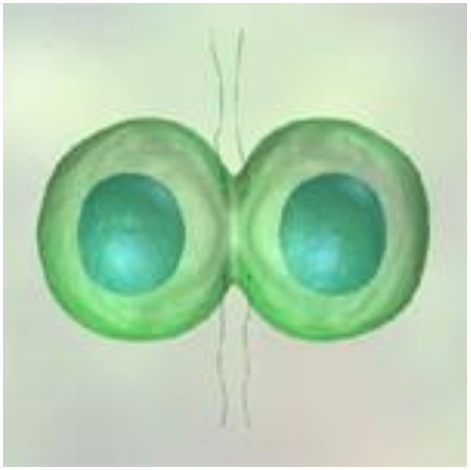
Deconstructing Darwinian Selfishness
Cooperation and the Evolution of Sex

Evolution of gamete size dimorphism

- Anisogamy: small sperm, large eggs
- Isogamy: Mating types without size differences
  - Some algae, fungi, protists

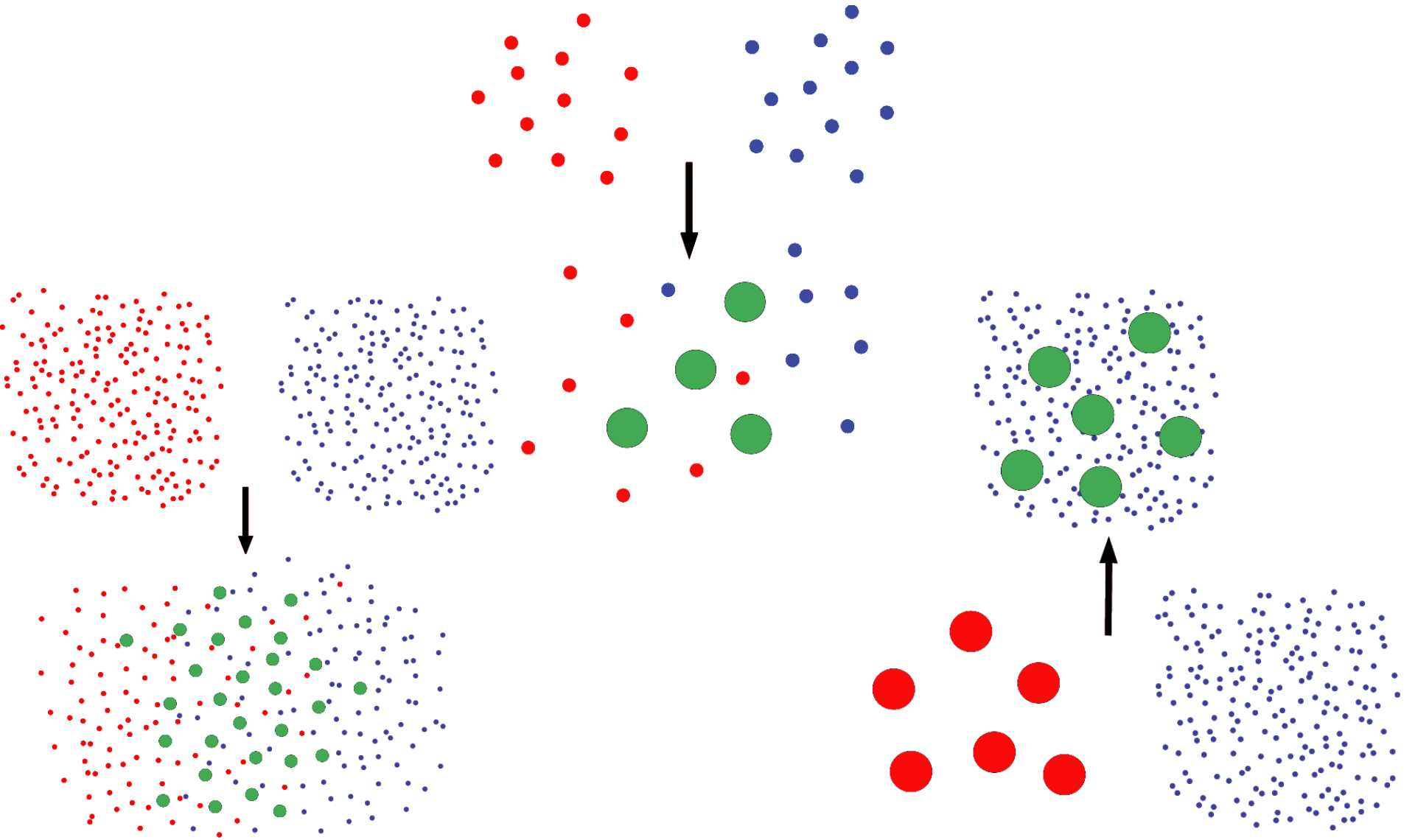




Model for the evolution of anisogamy

- Single gene coding for both egg and sperm sizes in a population of hermaphrodites
- Gamete size trades off with the number of gametes
- Large zygotes are more likely to survive

- Anisogamy maximizes the probability of formation of large zygotes



- No need for conflict, even in original model
- Life-history correlates of isogamy and anisogamy

Iyer and Roughgarden (2008) Theor. Popn. Biol. 73: 461–472

Separation of the sexes

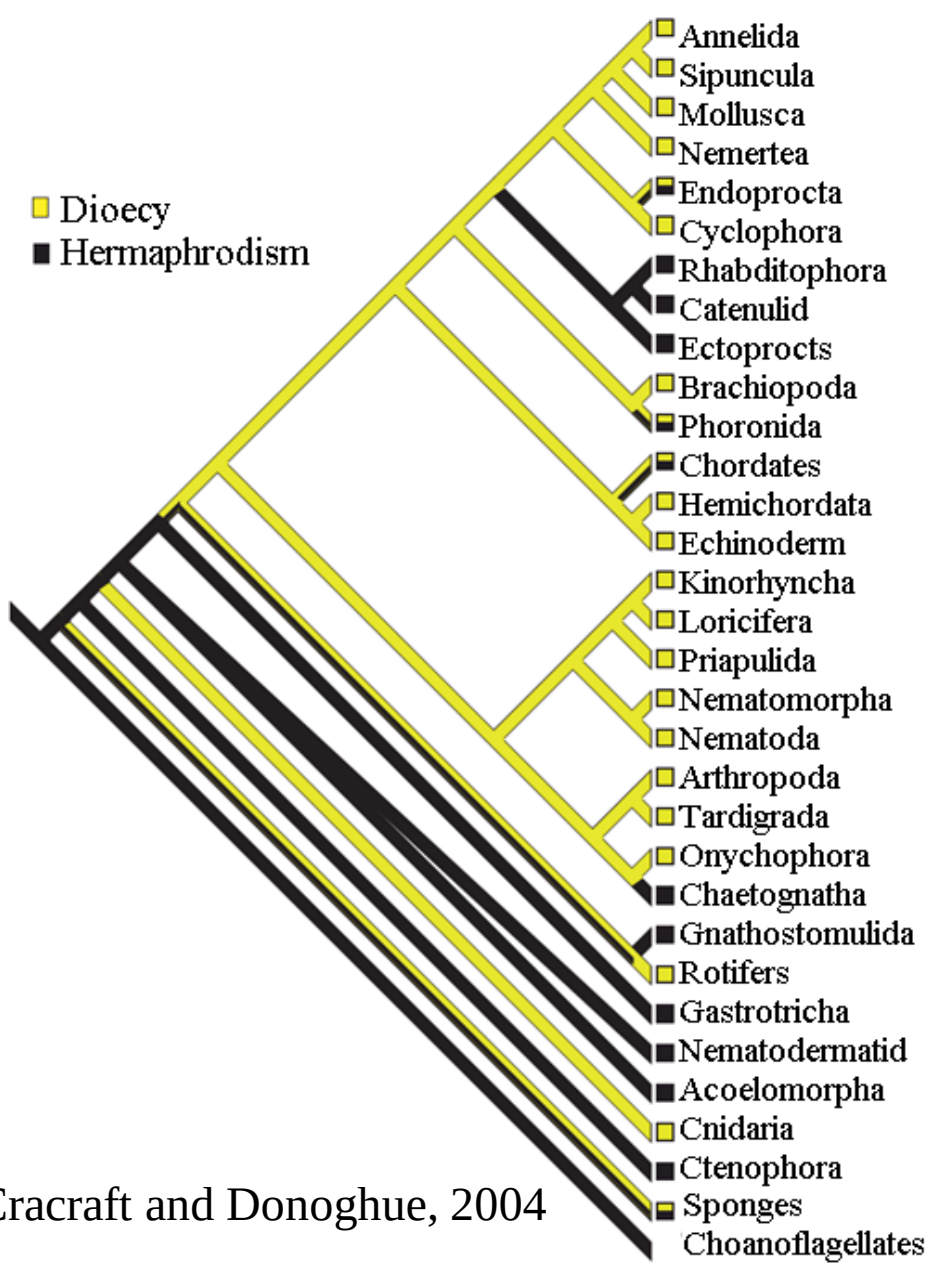
- Simultaneous hermaphrodism occurs in 70% of metazoan phyla
- 5-6 % species (or 1/3rd of all non-insect species) hermaphroditic; rest dioecious.

Dioecy: primitive or derived?

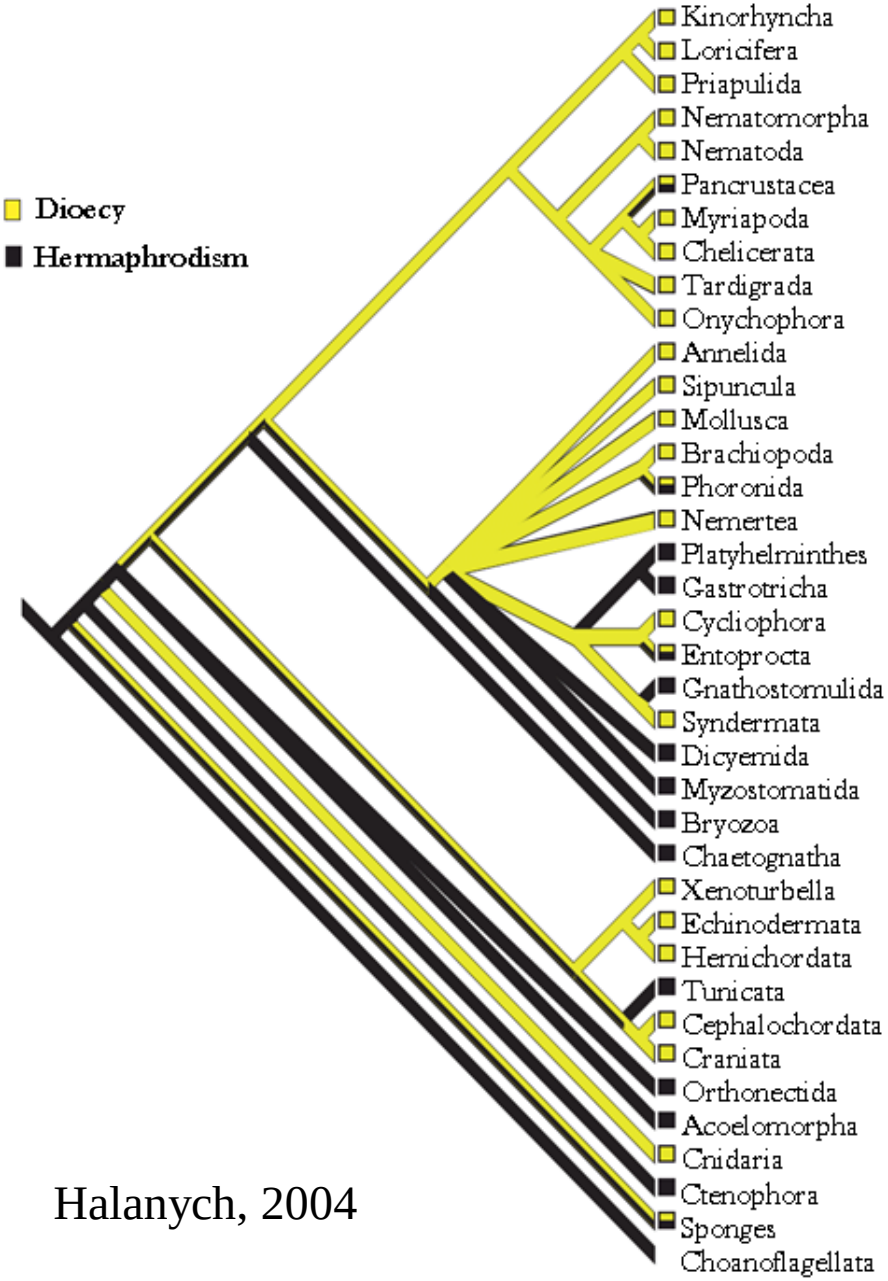
- Parker (1972), Ghiselin (1969): dioecy primitive, hermaphrodism derived
  - Benefits of selfing, mate location

- Data upto the family level to classify each phylum as hermaphroditic/ dioecious/ both
- Map on phylogenetic trees of metazoans

Ancestral trait reconstructed using maximum parsimony method (*Mesquite*)



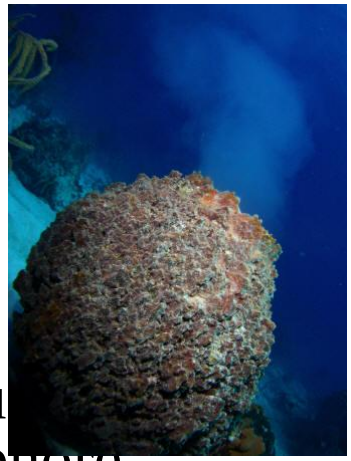
Cracraft and Donoghue, 2004



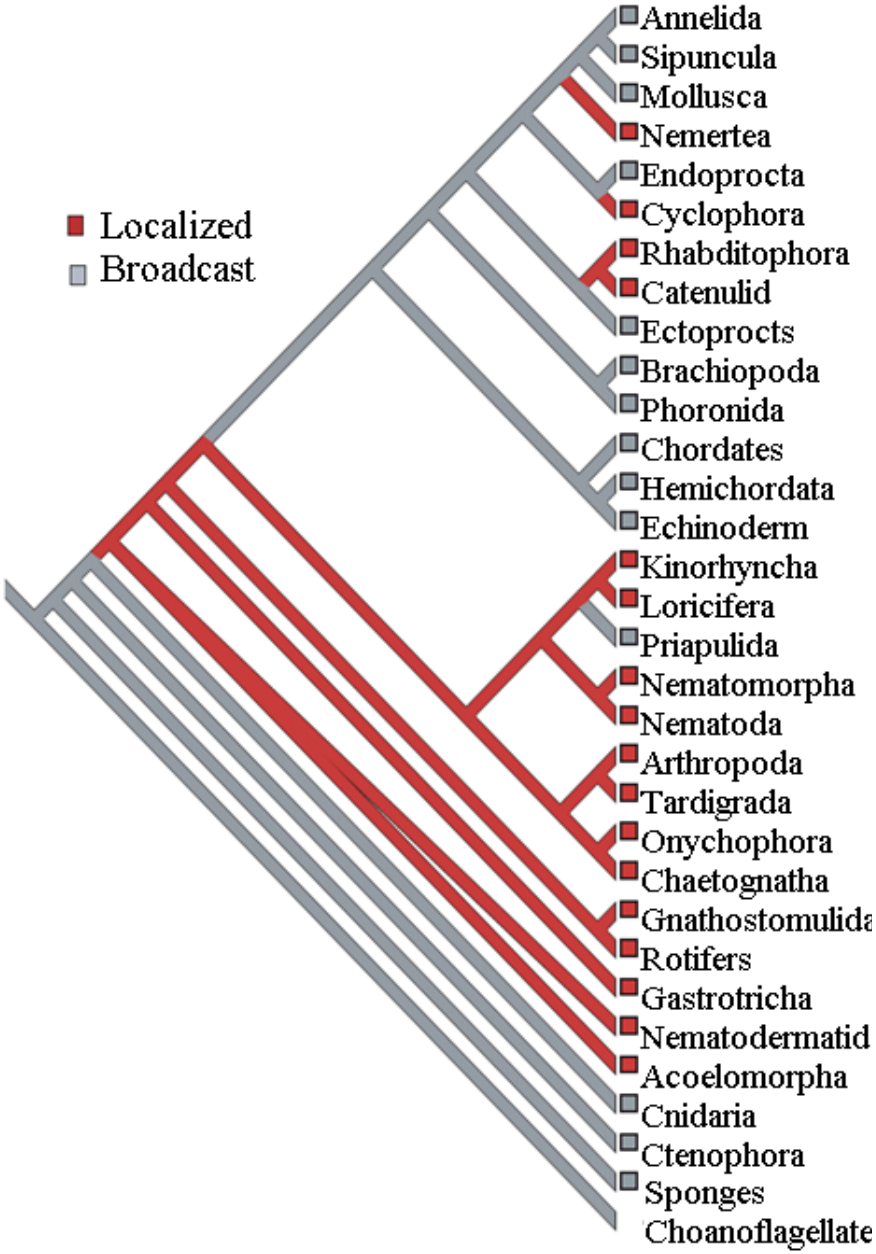
Halanych, 2004

What selects for dioecy?

- Trade-off between investments in male and female functions (Charnov, 1982)
- Avoiding inbreeding



- Fertilization behavior:
  - Broadcast spawning/ spermcasting
  - Localized fertilization (internal fertilization, pseu
    copulation, hypodermic impregnation, spermatophore
    release, etc.)



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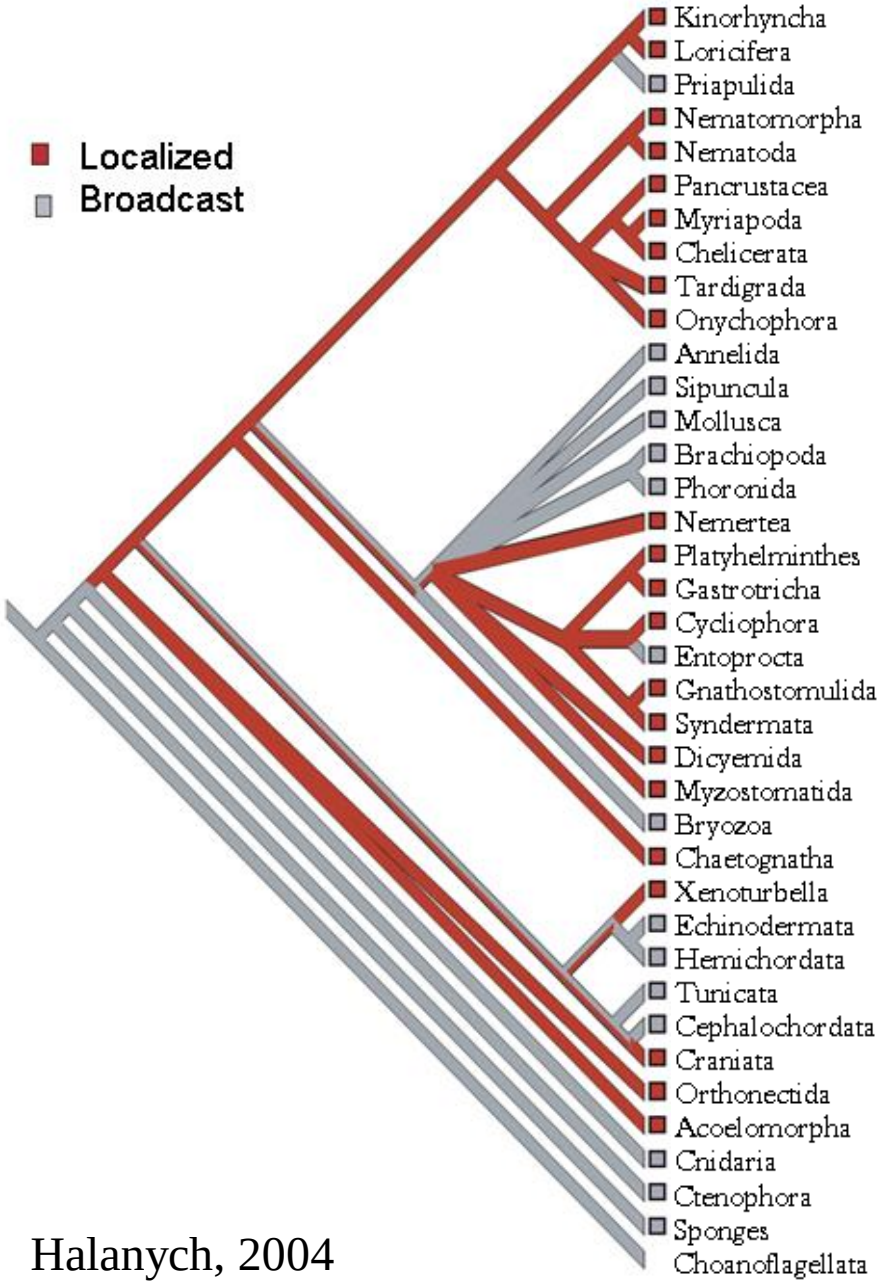
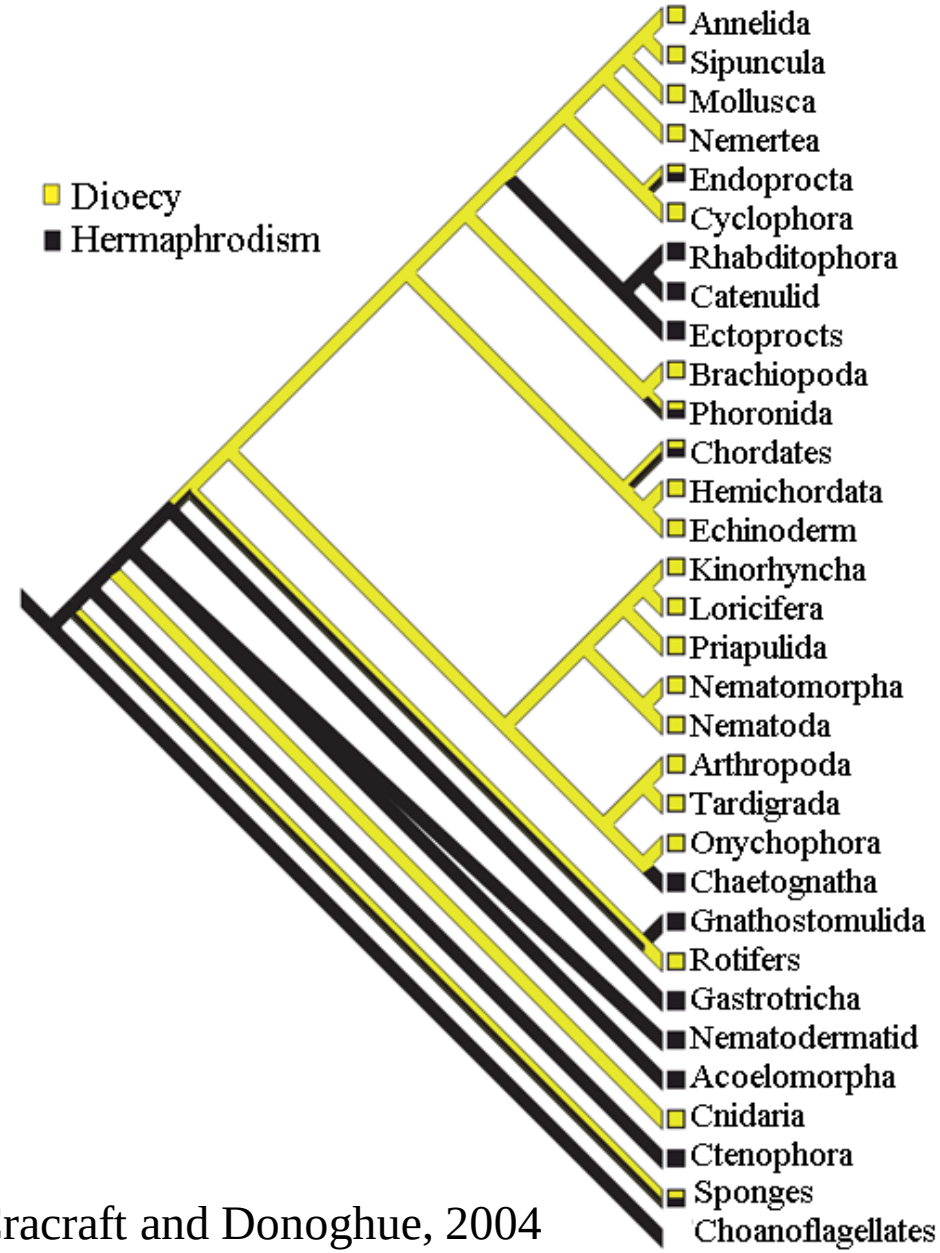
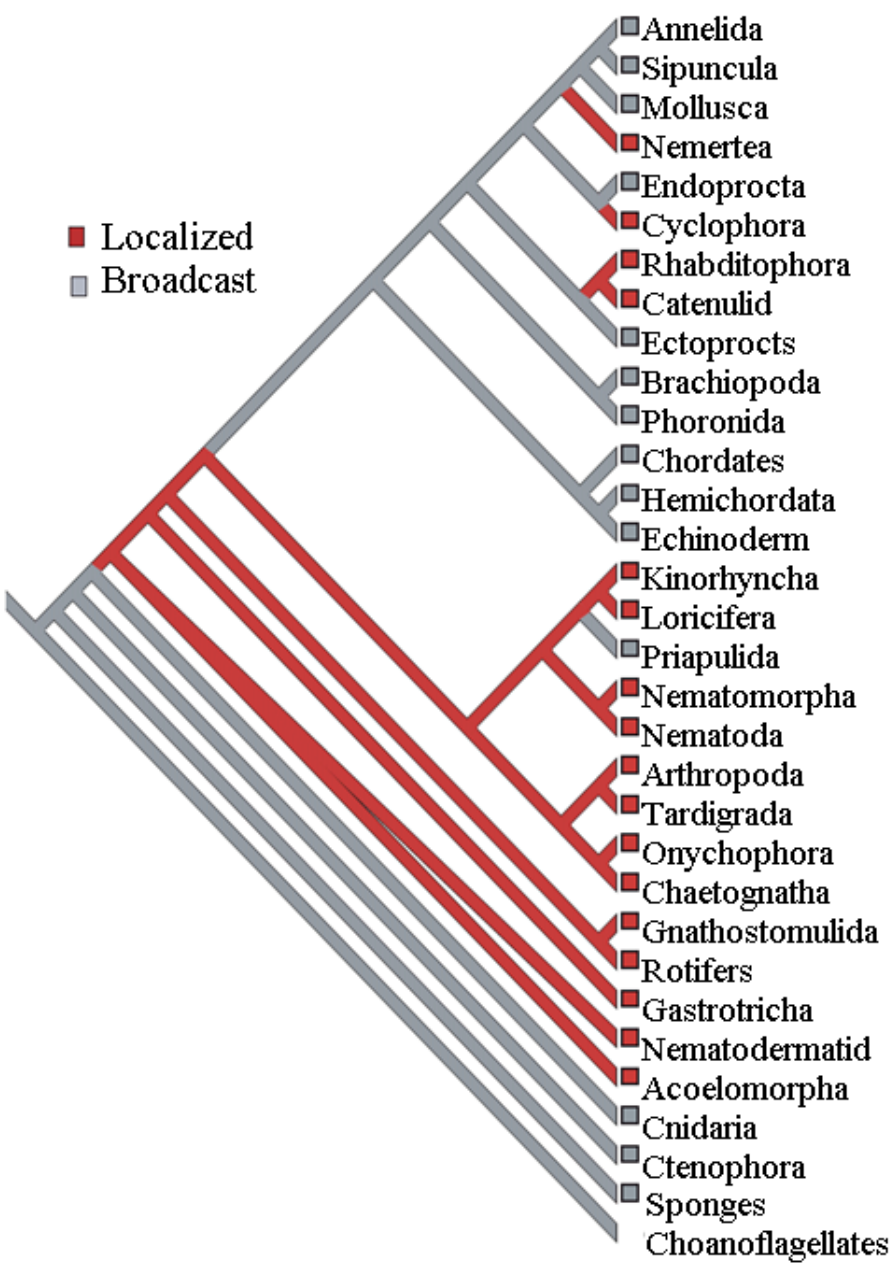


Halanych, 2004





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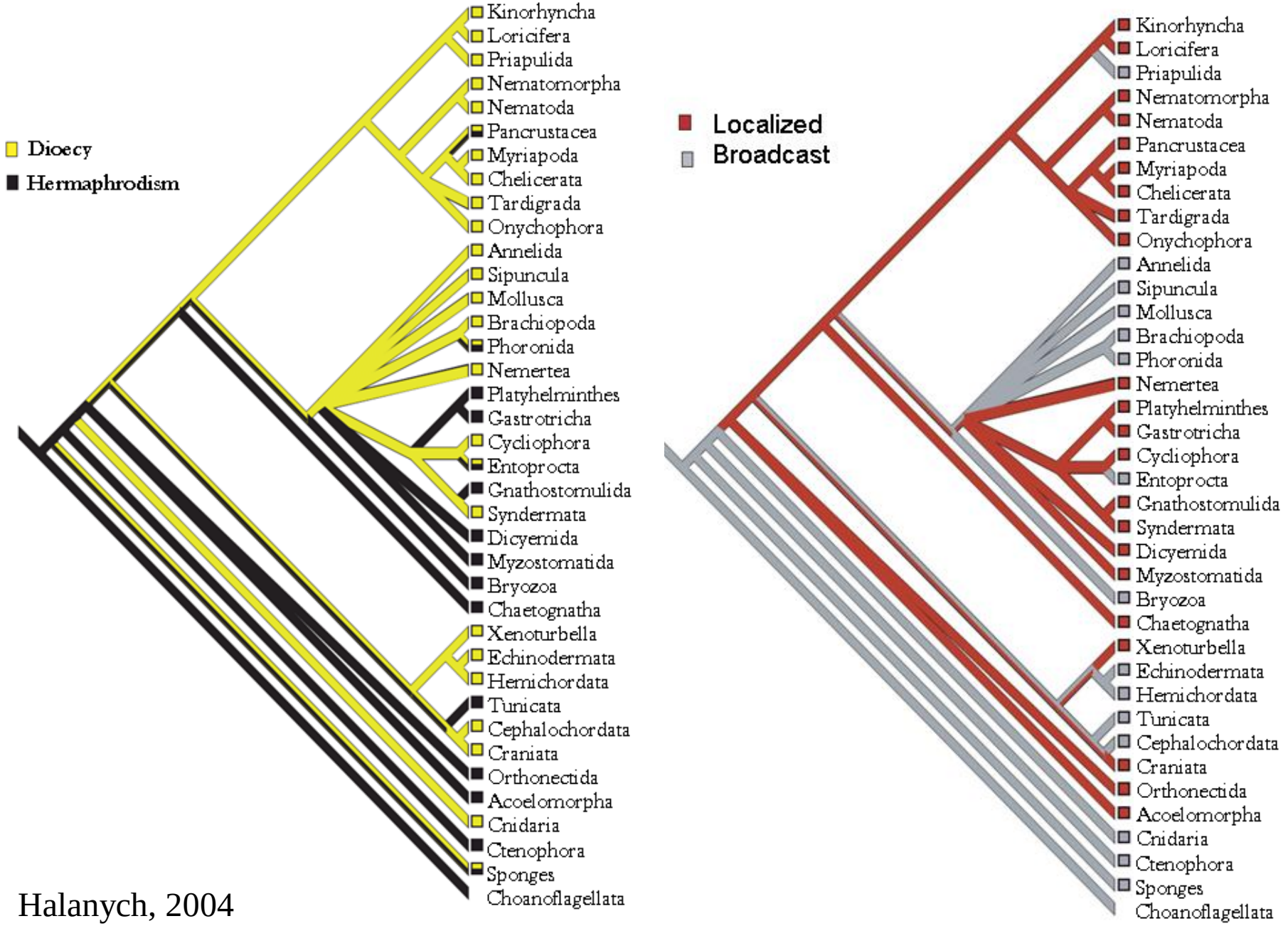


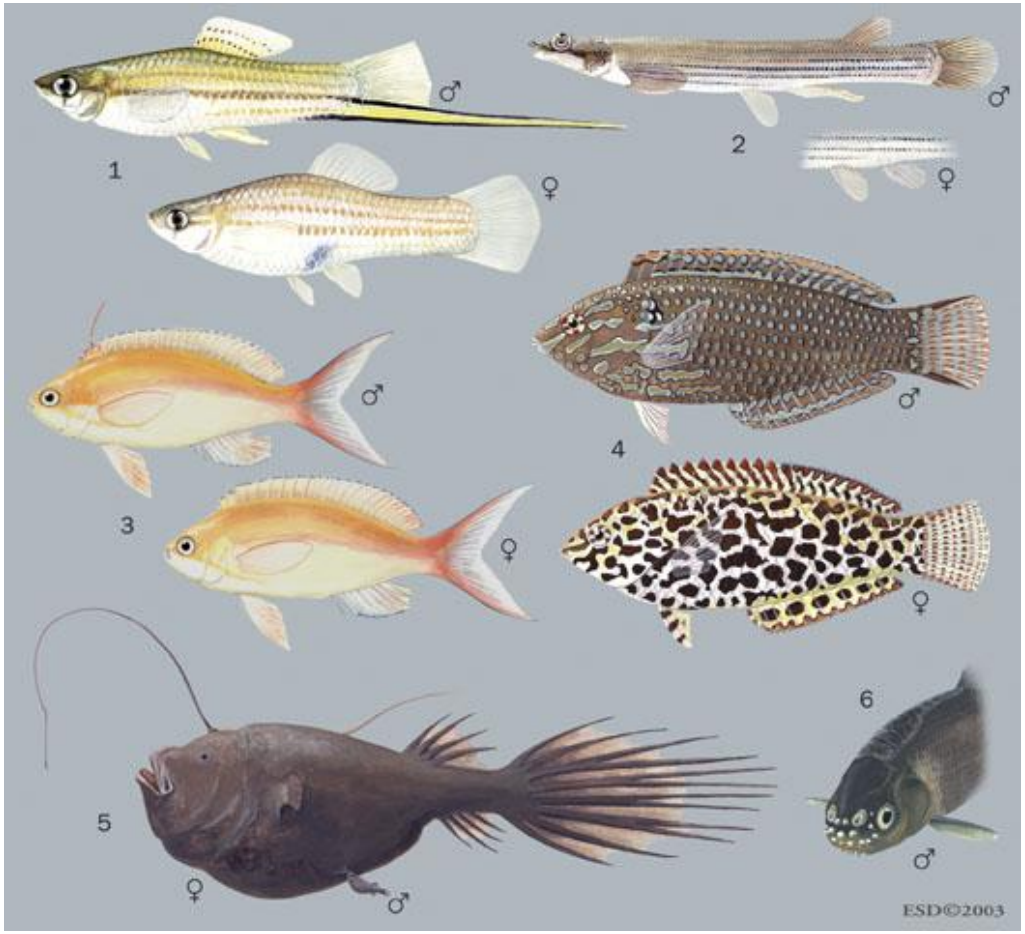
Halanych, 2004

Hypothesis: the two trends may be coupled

If sperm delivery increases fertilization probability, but carries a cost, specialization is favored.

- Sexes: specialization to increase fertilization probability, hence fitness of both morphs
- Specialization favoured under conditions of increased mobility, density or resource availability

Iyer & Roughgarden (2008) Evol. Ecol. Research, 10: 867–892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Role of morphological traits in social interactions

- Function of same-sex mating: social inclusion
- Same with elaborate ornamentation?

- A simple model for the advantage of social inclusion, and the evolution of ornaments as bids for it

Overview of model

- Two-tiered model: behavior and evolution
- Behavior to form coalitions to competitively exclude others from resources should be selected
- In this social context, ornaments can bid to join the better coalition

n individuals, R resources
Each initially has R/n

Coalition of 8 against 4: gain nothing if powerless

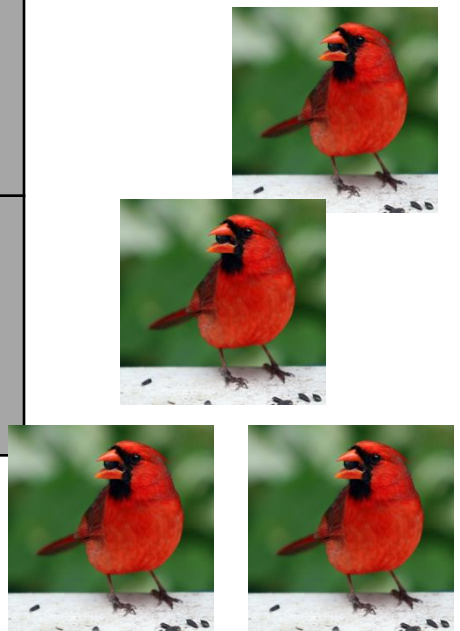
Payoff= *l* R/n

l

s

Coalition of 8 against 4: gain 4 if completely dominant

Payoff=
$(l+s)R/n$



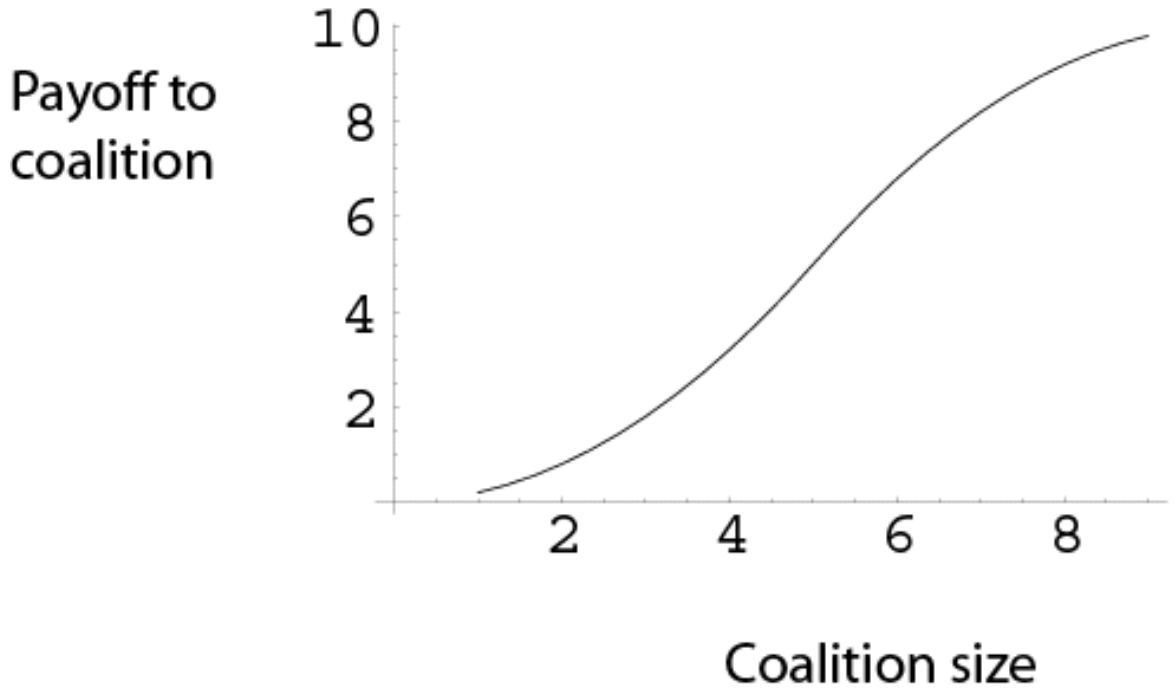
Intermediate case: power of coalition scales with relative difference in sizes

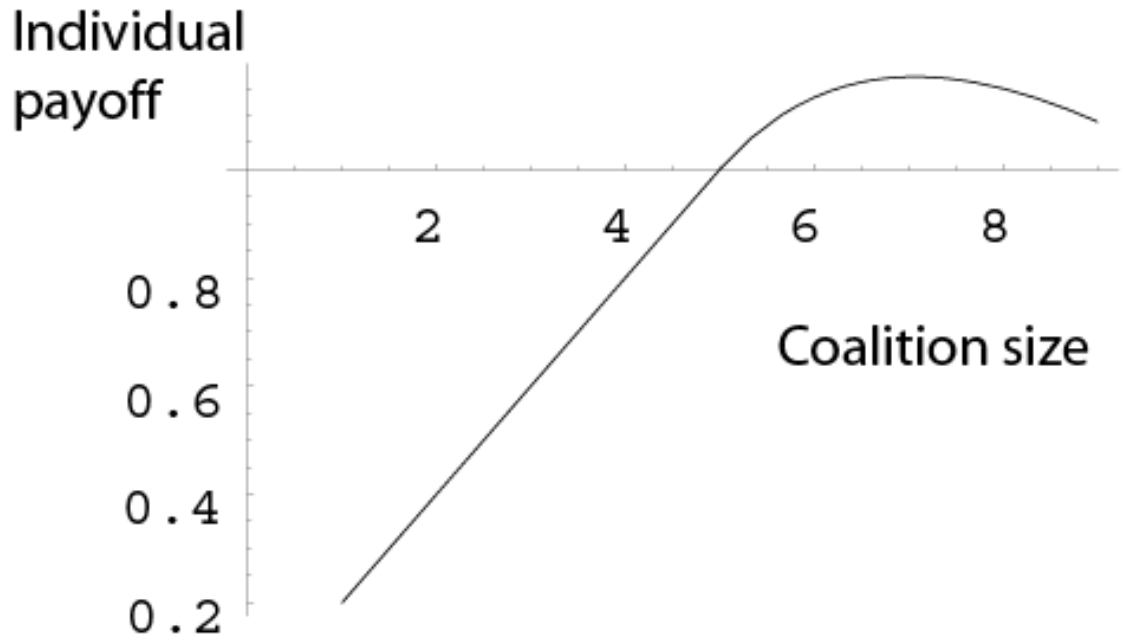
Payoff=

$$\frac{lR}{n} + \frac{l-s}{l+s}\frac{s\dot{R}}{n}$$

Payoff structure of the game

Stable coalitional structure: only two coalitions

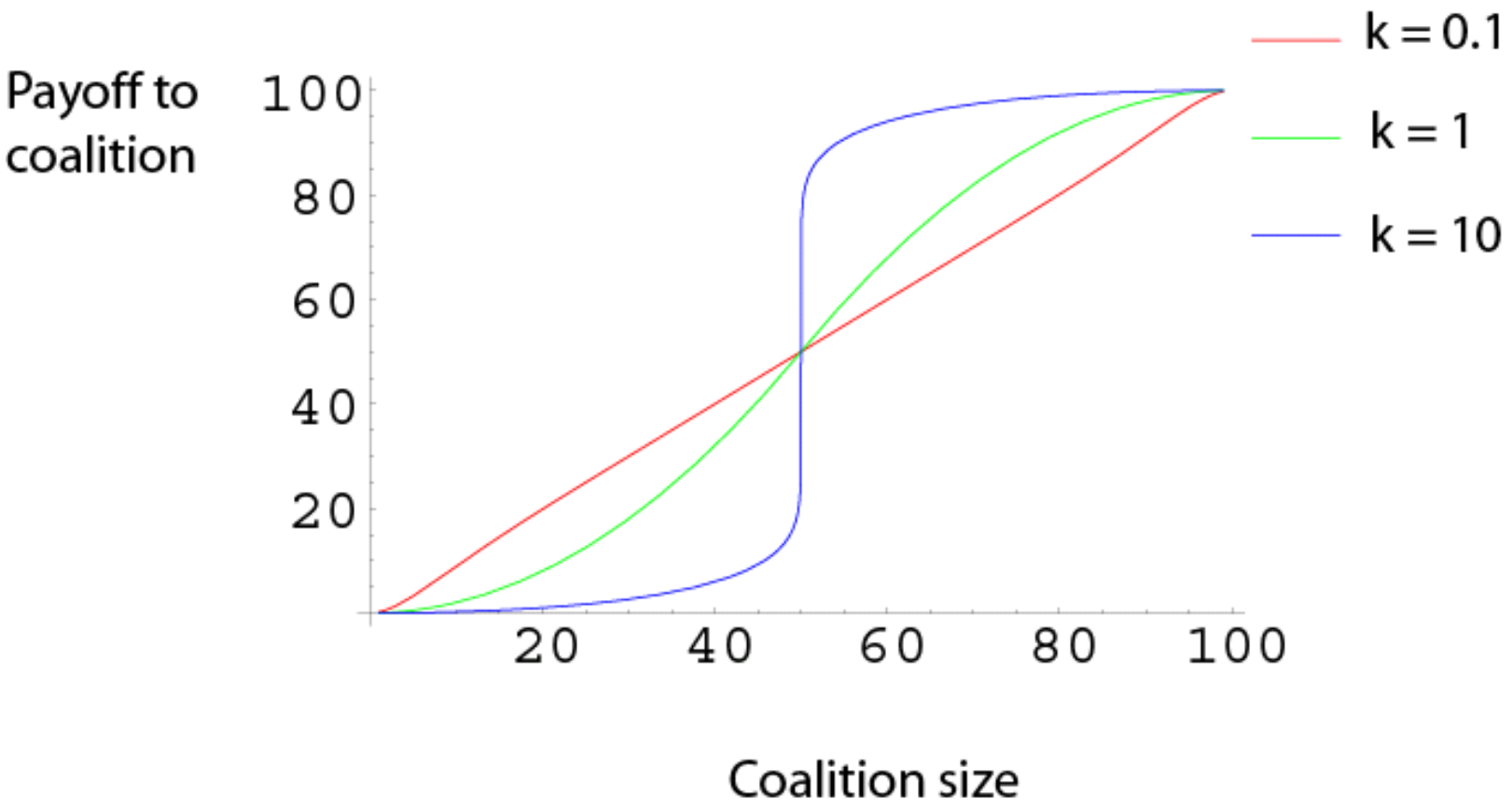




Larger coalitions obtain a larger share of a smaller pie -> optimal size of larger coalition

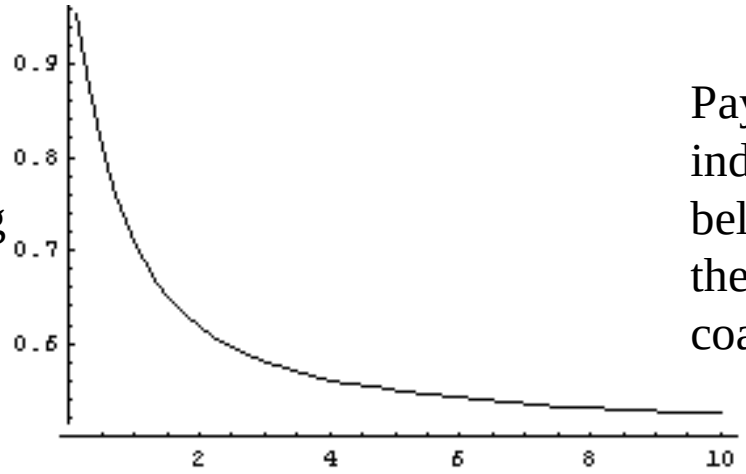
Vary the power of coming together to form a coalition

Payoff to larger coalition = $\frac{lR}{n} + \left(\frac{l-s}{l+s}\right)^{1/k} \frac{sR}{n}$



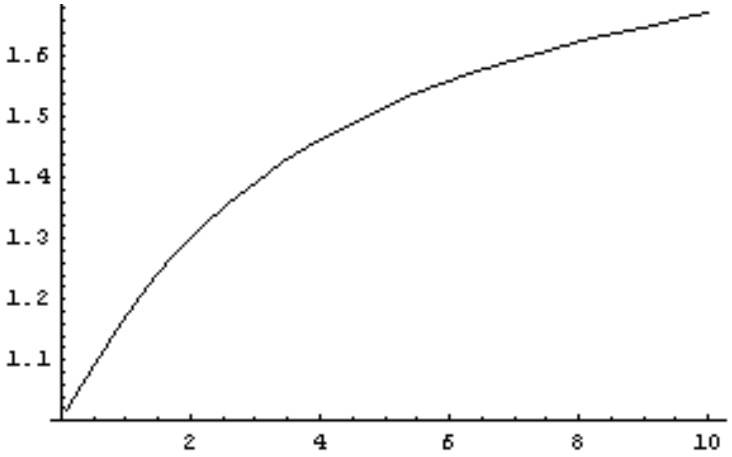
Power depends on resource distribution

Fraction of population constituting the larger coalition



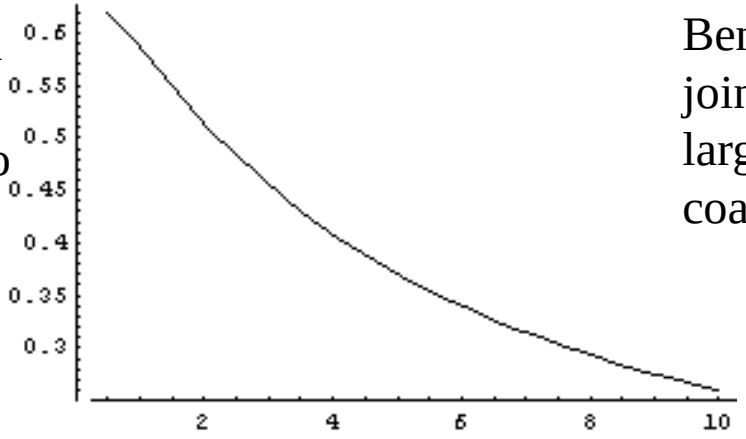
Power of coalition formation

Payoff to an individual belonging to the larger coalition



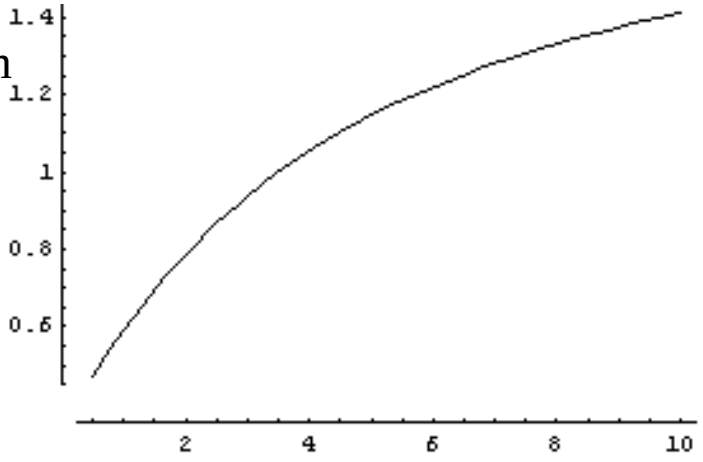
Power of coalition formation

Payoff to an individual belonging to the smaller coalition



Power of coalition formation

Benefit from joining the larger coalition



Power of coalition formation

Function of ornaments in this social context

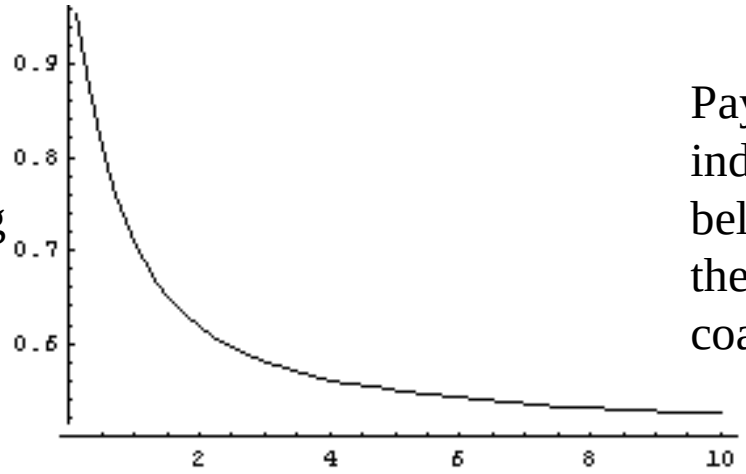
1. signal membership to avoid further conflict

2. bids to join the coalition
   - Maximum possible bid =

   Minimum {payoff when in smaller coalition,

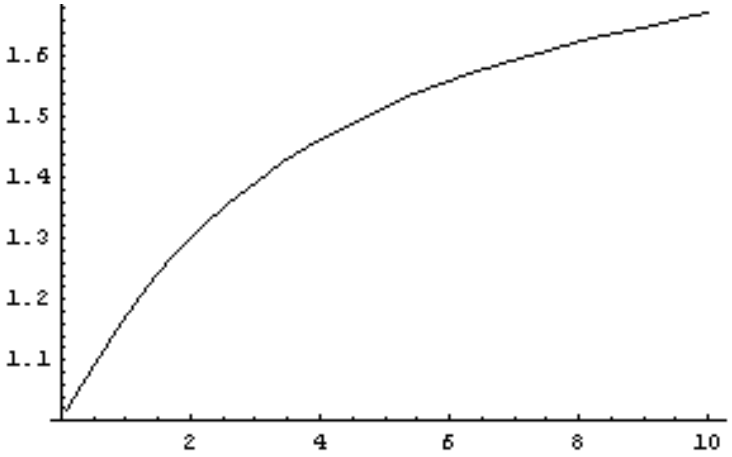
   benefit from joining the larger coalition}

Fraction of population constituting the larger coalition



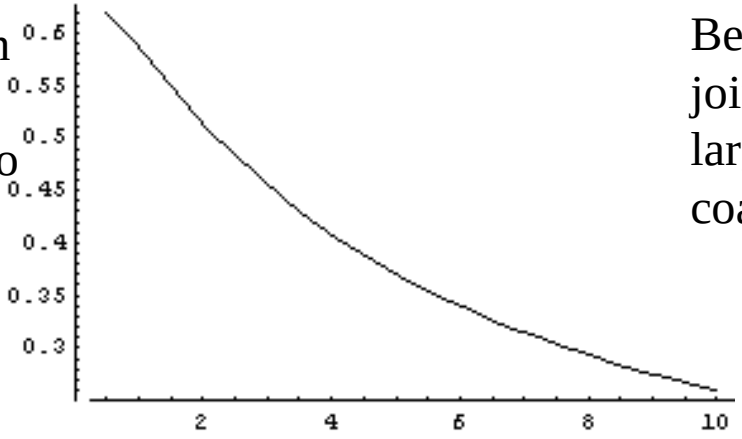
Power of coalition formation

Payoff to an individual belonging to the larger coalition



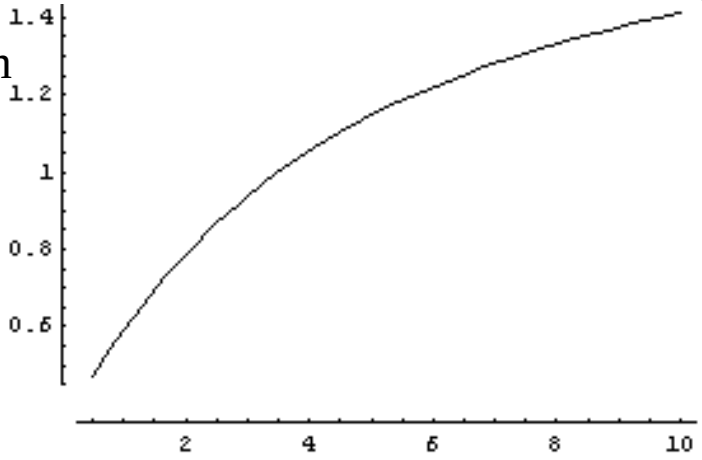
Power of coalition formation

Payoff to an individual belonging to the smaller coalition



Power of coalition formation

Benefit from joining the larger coalition



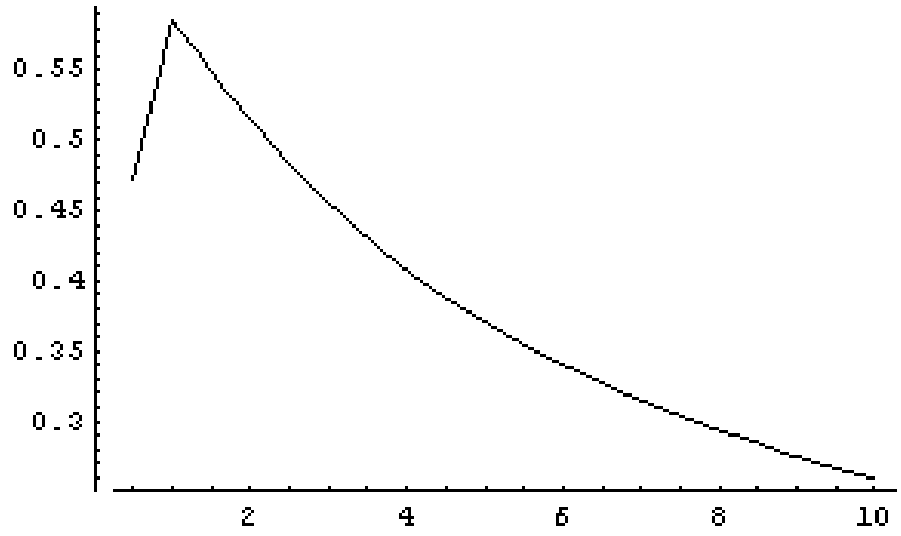
Power of coalition formation

Modeling the evolution of bid size

Individuals bidding higher more likely to join the clique…

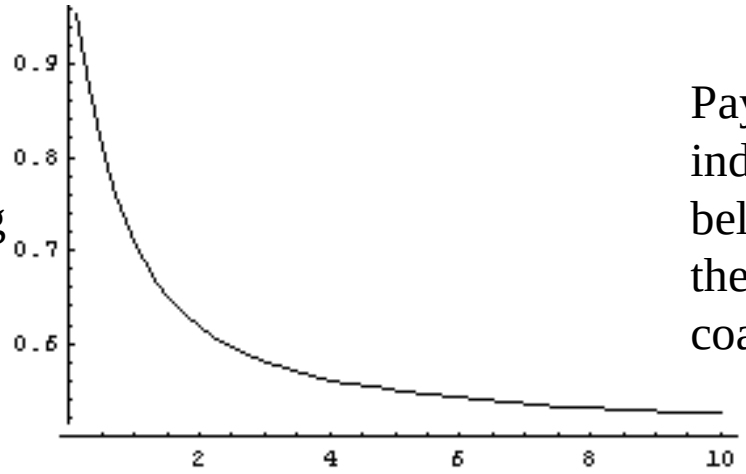
- Model invasion by mutants that make a different bid (higher, lower, no bid)
- Optimum bid-size
- Polymorphism between bidders and non-bidders

Cost of the bid



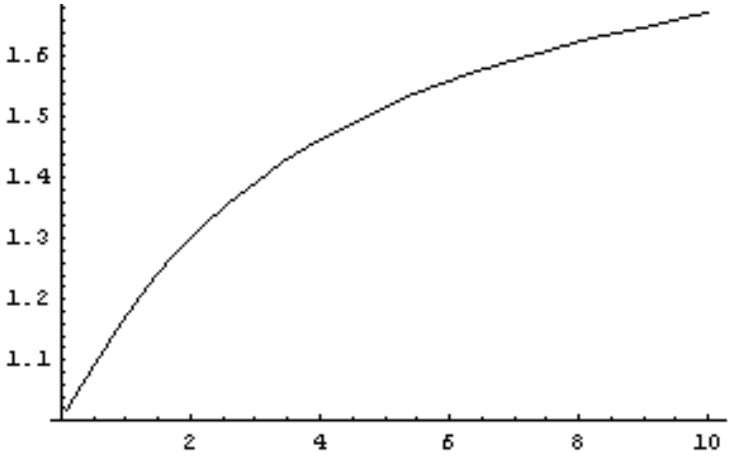
Power of coalition formation

Fraction of population constituting the larger coalition



Power of coalition formation

Payoff to an individual belonging to the larger coalition



Power of coalition formation

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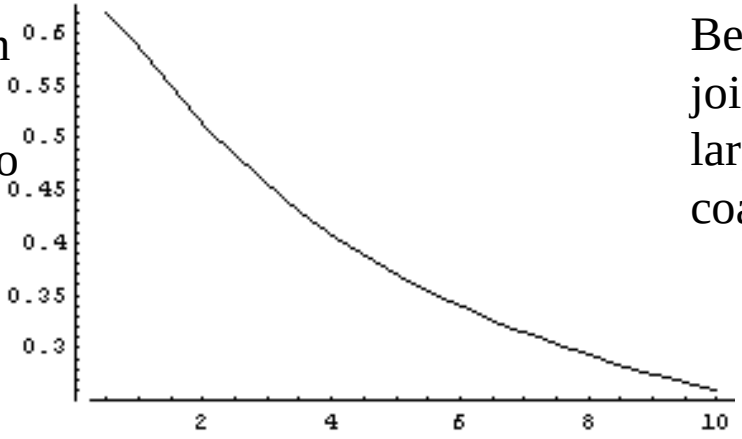
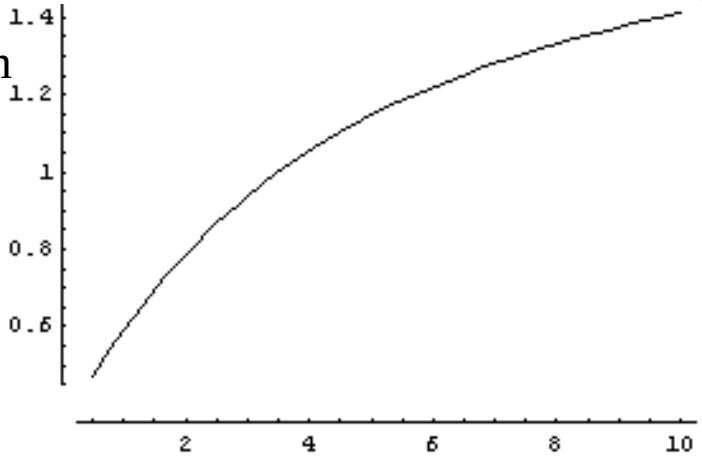


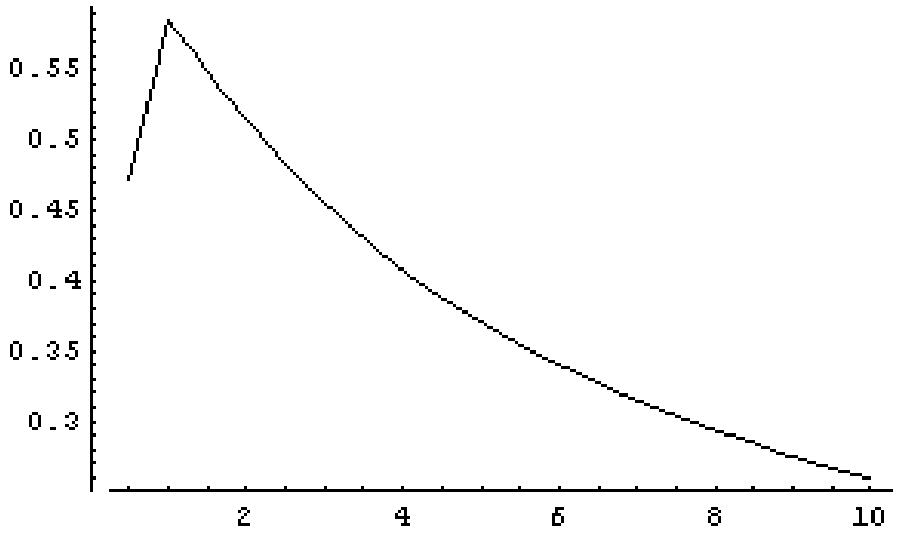
Power of coalition formation

Benefit from joining the larger coalition



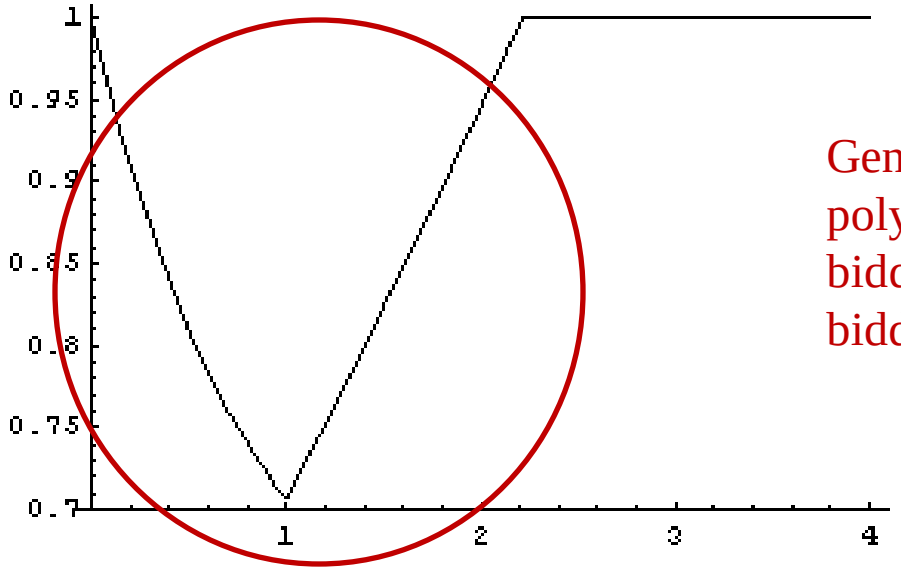
Power of coalition formation

Cost of the bid



Power of coalition formation

Fraction of the population bidding



Genetic polymorphism of bidders and non-bidders

Power of coalition formation

Predictions about size of ornament and fraction of population ornamented as functions of the ability of coalitions to control resources

Empirical support

Correlation between ornamentation and access to resources

Evolution of sexual phenotypes

- Whether males or females or both ornamented depends on species-specific optimal sex roles
- Coordination of parental investment as a pair
  - Selects for male investment during egg-laying phase
  - Defense of territory or resources by males, use of ornaments
  - Consistent with the evolutionary transitions from no care to male only care to biparental care in fish and birds

Evolution of sexual phenotypes

- Males could also form coalitions to dominate access to females

Evolution of sexual phenotypes

- Sexual monomorphism:
  - neither sex ornamented (no coalitions; k=0) or
  - both belong to same coalitions
- Sexual dimorphism: sex role specialization with coalition formation in at least one sex
- Polymorphism: intra-sexual variation in ornamentation, when resources more widely distributed

- Consistent with the diversity of sex roles and patterns of ornamentation

Tests of the model

- Do species form coalitions to control territory and resources?
- Evidence for correlation between
  - Resource distribution and ornamentation?
  - Tasks in parental care and monomorphism/ dimorphism?

- Future directions: theory for sex-roles in parental care

- Social dynamics: acquiring and trading opportunities to reproduce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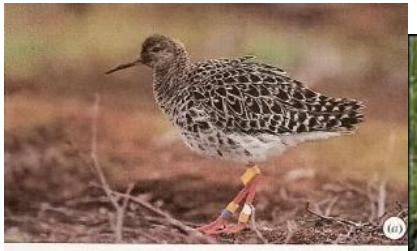

- Social dynamics: acquiring and trading opportunities to reproduce
- Complex, non-linear
- Outcomes of the dynamics may be uncertain, hard to predict
  - Perhaps the reason for the diversity in sex roles, reproductive strategies, morphs

Theoretical tools

Can borrow from political science, economics:

- Principal-agent games, theory of mechanism design
- Evolution as the principal/ social planner; social institutions help increase efficiency

Acknowledgements

Joan Roughgarden

Faculty and friends at Stanford University

Organizers, ICTS