

## Inclusive fitness and MLS

1. What is MLS and kin selection?
2. Averaging fallacy versus an expanded framework.
  - What is individual selection?
3. What is "r" and is it useful?
4. Predictive versus explanatory frameworks.

## What is the actual selection pressure behind kin selection?

- Consider a single family
- Consider multiple families
- Now, what is responsible for altruism?
- Is relatedness important or is selection at the group level important?
- Why did Hamilton miss this?

## Averaging fallacy

- George Price (1970, 1972)  $\Delta z = \frac{Cov(w, z)}{\bar{w}} + \frac{Cov(W, Z)}{\bar{w}}$
- Price equation partitions total gene frequency change into within and between group components.
- Hamilton later recalled of Price: "I am pleased to say that, amidst all else that I ought to have done and did not do, some months before he died I was on the phone telling him enthusiastically that through a "group-level" extension of his formula I now had a far better understanding of group selection acting at one level or at many than I had ever had before." (Hamilton 1996).

## Averaging fallacy

Figure 5.5:  $M$  is an evolving metapopulation that is divided into groups, which contain organisms, which contain genes. MLS theory and conventionalism assign different meanings to "individual selection" and "genetic selection." They agree about what "group selection" means.

	MLS theory	Conventionalism
Group selection	Variation in the fitnesses of groups in $M$	Variation in the fitnesses of groups in $M$
Individual selection	Variation in the fitnesses of organisms within groups	Variation in the fitnesses of organisms in $M$
Genetic selection	Variation in the fitnesses of genes within organisms	Variation in the fitnesses of genes in $M$

Group selection is averaged in to what is considered "individual and even genetic selection". What evolves in the population is still the trait that confers the highest per capita fitness.

### Did Darwin write the *Origin* backwards?

Philosophical Essays on Darwin's Theory  
Elliott Sober

## Expanded versus reductionist frameworks

Figure 5.4: An individual's fitness depends on its own phenotype and on the phenotype of its partner.

the individual is	the individual's partner is	
	Altruistic	Selfish
Altruistic	$x+b-c$	$x-c$
Selfish	$x+b$	$x$

- (1) There is group selection favoring altruism and individual selection favoring selfishness, and the former cause is stronger than the latter <sup>15</sup>
- (2)  $\Pr(\text{partner is } A \mid \text{individual is } A) - \Pr(\text{partner is } A \mid \text{individual is } S) > c/b$ .

$$w(A) = \Pr(\text{partner is } A \mid \text{individual is } A)(x-c+b) + \Pr(\text{partner is } S \mid \text{individual is } A)(x-c)$$

$$w(S) = \Pr(\text{partner is } A \mid \text{individual is } S)(x+b) + \Pr(\text{partner is } S \mid \text{individual is } S)(x)$$

Let  $p = \Pr(\text{partner is } A \mid \text{individual is } A)$  and let  $q = \Pr(\text{partner is } A \mid \text{individual is } S)$ . Then  $w(A) > w(S)$  precisely when

$$p(x-c+b) + (1-p)(x-c) > q(x+b) + (1-q)x.$$

$$(3) w(A) > w(S) \text{ if and only if } \Pr(\text{partner is } A \mid \text{individual is } A) - \Pr(\text{partner is } A \mid \text{individual is } S) > c/b.$$

The inclusive fitnesses of the two traits are

$$I(S) = x$$

$$I(A) = x - c + rb,$$

from which it follows that

$$(4) I(A) > I(S) \text{ if and only if } r > c/b.$$

Two frameworks are the same when:

$$(5) r = \Pr(\text{partner is } A \mid \text{individual is } A) - \Pr(\text{partner is } A \mid \text{individual is } S).$$

\*\*\*Note that any distinction between fitness within and between groups is now lost in the inclusive fitness formulation\*\*\*

## Why “r” may be different

- If the gene in question is close to fixation in the population, full sibs will still be  $r=0.5$
- If the gene in question is dominant.

Figure 5.7. If an individual is altruistic (*A*) or selfish (*S*), and if *A* is rare (or common), what is the individual's probable genotype? What is the probable genotype of its parents? And how probable is it that its partner is *A*? The partner is the individual's full sibling and altruists have genotype *aa* or *as* while selfish individuals have genotype *ss*.

	Probable genotype for individual	Probable genotype for individual's parents	Pr(partner is <i>A</i>   -)
individual is <i>A</i> , <i>A</i> is rare	<i>as</i>	<i>as</i> x <i>ss</i>	0.5
individual is <i>S</i> , <i>A</i> is rare	<i>ss</i>	<i>ss</i> x <i>ss</i>	0
individual is <i>A</i> , <i>A</i> is common	<i>aa</i>	<i>aa</i> x <i>aa</i>	1
individual is <i>S</i> , <i>A</i> is common	<i>ss</i>	<i>as</i> x <i>as</i>	0.75

## What is “r” now and do we care?

- Hamilton noted this issue and realized in 1975, that “r” is not what is important, it is merely that altruists interact with other altruists.
- “r” changed to the probability of sharing the gene (not necessarily IBD)
- “r” then changed again to now to represent phenotypic correlation. Thus “kin” is no longer a necessary part of kin selection. (Genes are not even necessary).
- Relatedness (kinship) is merely a way to partition variance amongst groups, however other partitioning process also achieve this.

## In a nutshell

“The only difference [between] inclusive fitness [and MLS] is that instead of calculating the effects *from a focal individual* to its reproduction and that of neighbors, fitness accounting is done all in terms of effects *to the focal individual's* reproduction from itself and its neighbors.”

A Defense of Sociobiology

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## Predictive value of the frameworks

- “r” provides no value at point of inquiry, but useful when interpreting results (Gardner).
- “Hamilton's rule is at worst superfluous and at best ad hoc” (Nowak et al. 2010)
- When only considering net outcomes, all traits are classified as acting in self-interest.

## Eusociality: Origin and consequences

Edward O. Wilson\*\* and Bert Hölldobler<sup>15</sup>

- Close relatedness either precursor or result.
- Evidence from presocial species suggest low relatedness in colony founding queens.

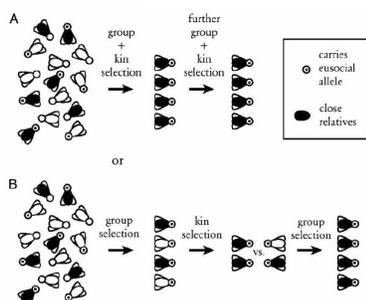


Fig. 1. The two competing hypotheses of the origin of eusociality in insects and thence before the point of no return. The first (A) holds that in the earliest stage, kin selection is binding, making close relatedness a key feature; if combined with group selection, kin selection favors primitively eusocial colonies in a population of solitary or presocial insects (far left). The second hypothesis (B), newly presented here, holds in contrast that group selection is paramount as the binding force, and kin selection is minor or absent as a binding force for the group as a whole and weakly dissulative if it forms competing groups. Relatedness, in hypothesis B, is increased as group selection cleanses the dissulative negotiism effect of kin selection. The empirical evidence appears to favor, but does not conclusively prove, B.

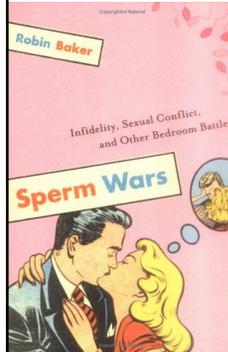
“In inclusive fitness [posits] that individuals are “trying” to maximize the representation of their genes in future generations, where it is recognized that an individual's genes can be found in her genetic relatives (non-relatives) as well as in her own offspring... The net result is that any helping behavior that evolves gets viewed as a form of genetic self-interest. This may seem like a pleasing consequence until it is realized that “self-interest” has now become an all-encompassing category. When altruism evolves, this is consistent with the heuristic idea of self-interest, since altruists are getting their altruistic genes into the next generation by helping other altruists. The idea that altruism is good for the group but bad for the individual has been lost. The way to recovery is to set aside the metaphor of “trying” and focus on the fact that there can be conflicts of interest between different levels of organization. What is good for the individual can conflict with what is good for the group. Our concept of adaptation should reflect this fact. Rather than use —individual adaptation as an all-encompassing label that is defined so that it applies to all adaptations regardless of whether they evolve by group or individual selection.”

-Elliot Sober (2010)

## Why is group selection still stigmatized?

- Hamilton acknowledged inclusive fitness was group selection in 1975, so why are his disciples unwilling to make this leap?
- What is group selection? Few know
  - Artifact of the widespread rejection in the 60s.
  - Understanding GS, came a distant second to the fact that it is impossible.
- Lead to the reemergence of GS under other names (pluralism).
  - Direct and indirect reciprocity, social selection, costly signalling, biproduct mutualism, etc...

## A novel application of MLS



- Sexual conflict, which refers to males and females acting against each other's interests.
- In a typical scenario, males best equipped to exploit females are favored locally over more prudent males, despite reducing female fitness (thus group fitness).

## Field dominated by within group selection

- Experiments typically take place within a single group OR disregarding group differences.
- These experiments demonstrate drastic population level consequences to this conflict (evolutionary suicide).
- Why are natural population entrenched in sexual conflict not going extinct?
- In multigroup populations, groups with less sexual conflict will contribute more offspring to the next generation than higher conflict groups, countering the local advantage of harmful males.
- Similar to the conflict between selfishness and altruism.

### Sex, death and tragedy

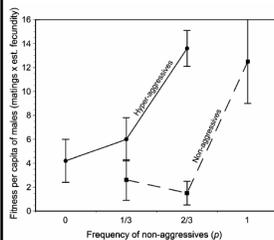
Daniel J. Rankin and Hanna Kokko

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## Water strider *Aquarius remigis*



## Within vs. between group selection



Pools	Low	High
Matings	46	30
Overall eggs laid	1058 [8.04]	1069 [6.72]
$\Delta$ eggs laid (%)**	-6.0	-40.0
Overall nymphs hatched	844 [6.41]	607 [3.81]
$\Delta$ nymphs hatched (%)*	-11.62	-40.93
Overall hatching success (%)	79.77	56.78
$\Delta$ Hatching (%)	-3.0	-0.1
female survival (%)	80.00	60.00
nymph survival (%)	14.81	8.14
Overall pool fitness**	0.950	0.311
$\Delta$ pool fitness (%)*	-11.62	-40.93

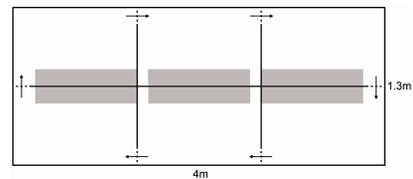
Behav Ecol Sociobiol  
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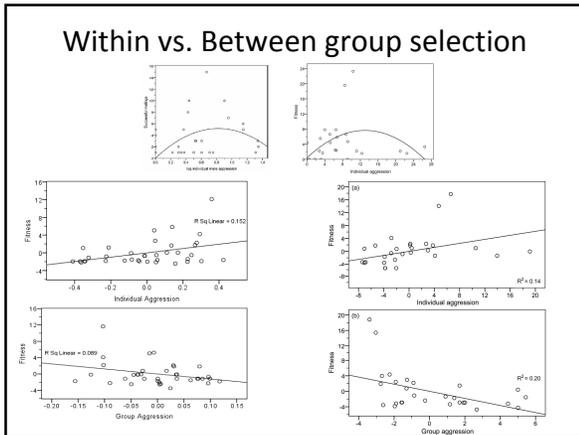
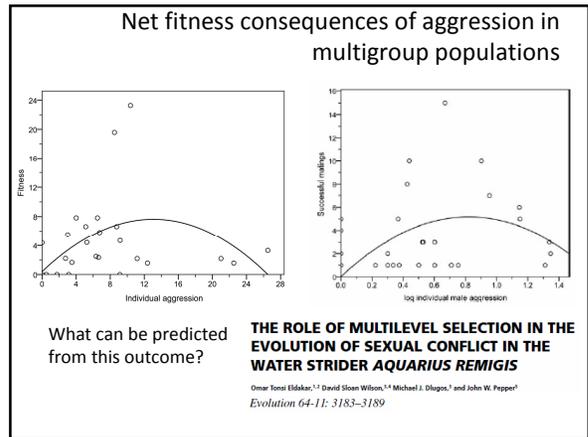
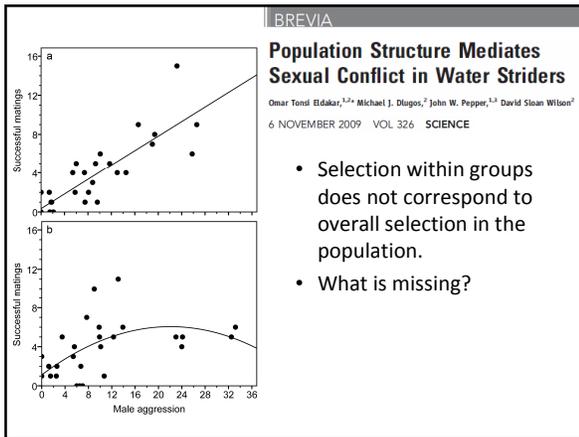
Aggressive mating as a tragedy of the commons in the water strider *Aquarius remigis*

Omar Tami Elidakar · Michael J. Dregus ·  
St. Simon Wilson · David Sloan Wilson

## Selection within groups vs. population



- Maximize variation in aggression within groups, eliminate variation between groups.
- Allow individuals to disperse in a multi group population.
- Compares fitness differentials within groups to what occurs in a naturalistic population.



### Summary

- Group selection cannot be evaluated based on the net outcome alone.
- Group selection can only be evaluated when within and between group selection differentials are calculated.
- Predictive value of calculating within and between group differentials.

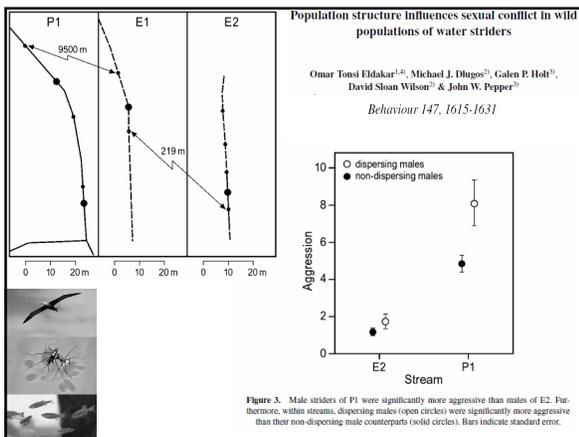


Figure 3. Male striders of P1 were significantly more aggressive than males of E2. Furthermore, within streams, dispersing males (open circles) were significantly more aggressive than their non-dispersing male counterparts (solid circles). Bars indicate standard error.