

female wasp lays eggs in fly pupae



Parasitic wasps often lay clutches with a female biased sex ratio.  
Why would this be advantageous?

In this system, when would it be advantageous to lay a clutch with an equal or even a male biased sex ratio?



wasp larvae develop  
and devour fly

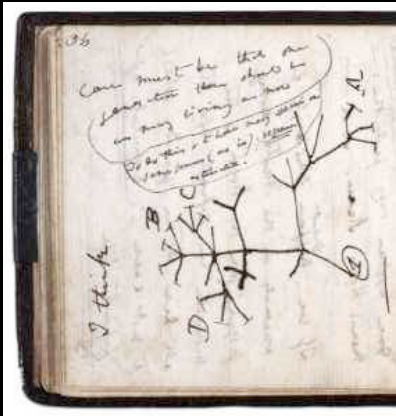


they emerge from fly  
pupal case ready to mate

ON  
THE ORIGIN OF SPECIES  
BY MEANS OF NATURAL SELECTION,



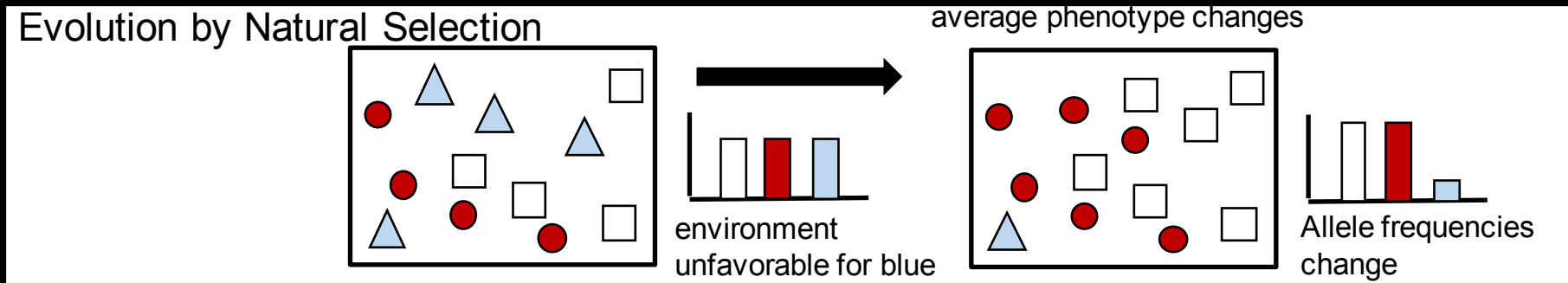
LONDON:  
JOHN MURRAY, ALBEMARLE STREET.  
1859.  
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# Darwinian Puzzle (Paradox)

# Selection and Evolution

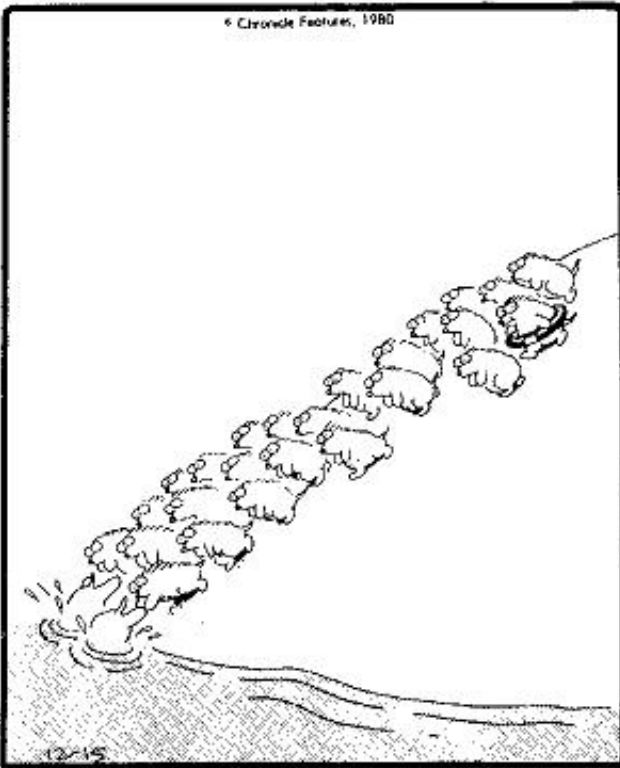
Natural Selection retains alleles that promote the individual's lifetime reproductive fitness.



# THE FAR SIDE

By GARY LARSON

© Chronicle Features, 1980



narrator Winston Hibler, “A kind of compulsion seizes each tiny rodent and, carried along by an unreasoning hysteria, each falls into step for a march that will take them to a strange destiny.”

## Geographical and Temporal Patterns of Lemming Population Dynamics in Fennoscandia

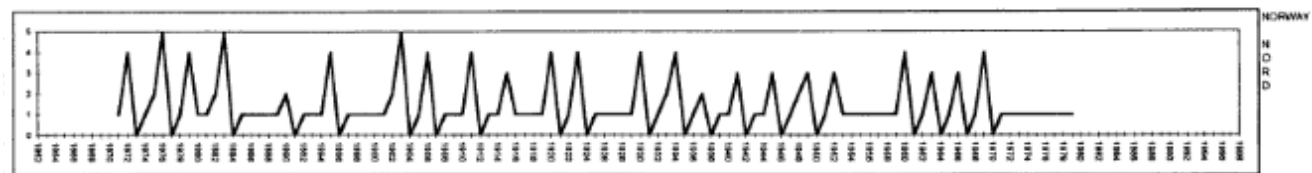
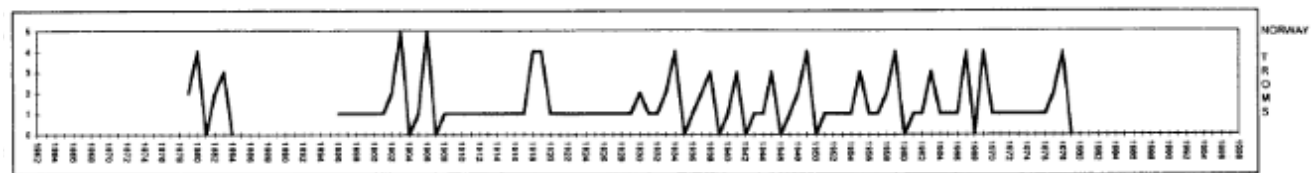
Anders Angerbjörn, Magnus Tannerfeldt and Håkan Lundberg

ECOGRAPHY

*Ecography*  
Vol. 24, No. 3 (Jun., 2001), pp. 298-308

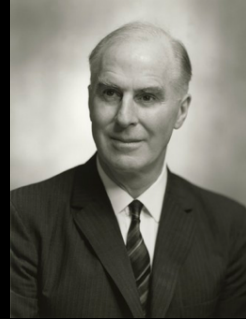
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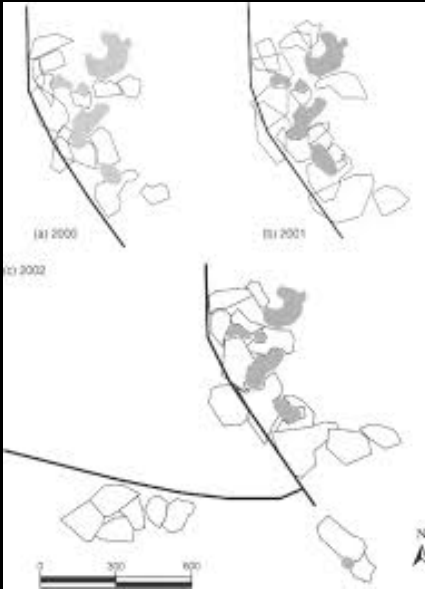




“Animal Dispersion in Relation to Social Behaviour”  
by Wynne-Edwards formally proposed “Group Selection”



“Adaptation and Natural Selection”  
by George C Williams countered with individual level selection



# Social Interactions

Recipient

Benefit

Cost

Donor

Benefit

Cost

cooperation	manipulation
altruism	spite



Alarm calls appear Altruistic?

Provide three alternative hypotheses that could explain this behavior could evolve through Natural Selection.

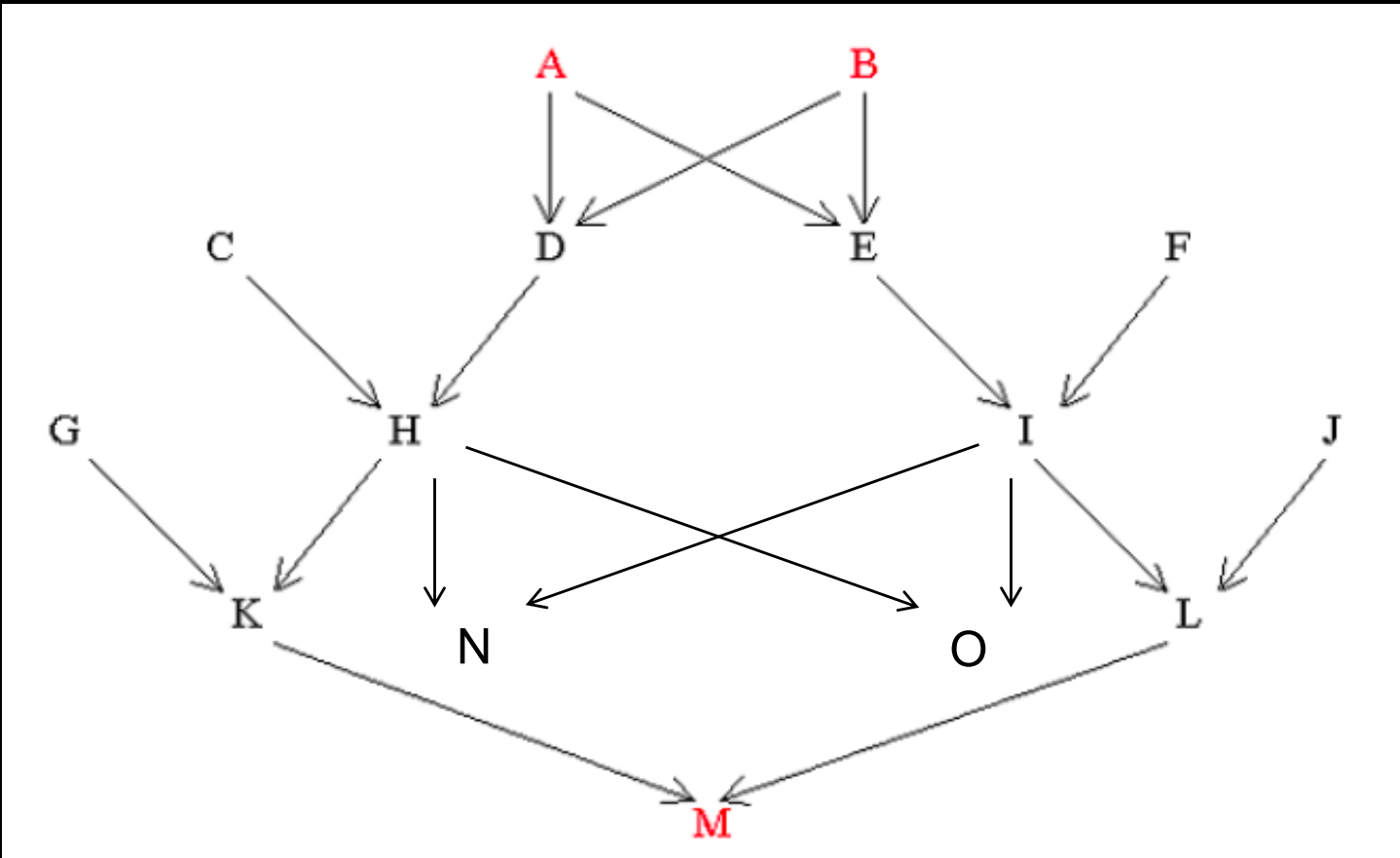


Natural selection will tend to increase a genetically based trait that is costly to the individual if that trait influences behavior that provides increased reproductive success to a sufficient number of individuals who share a sufficient amount of genetic material (on average).

W.D. Hamilton

direct fitness + indirect fitness = inclusive fitness

Hamilton's rule "Cooperation should happen when  $r_b B > C$



$$R(AL) = 1/8$$

$$R(DE) = 1/2$$

$$R(HI) = 1/8$$

$$R(AM) = 1/8$$

$$R(NO) = 9/16$$

$$R(KL) = 1/32$$



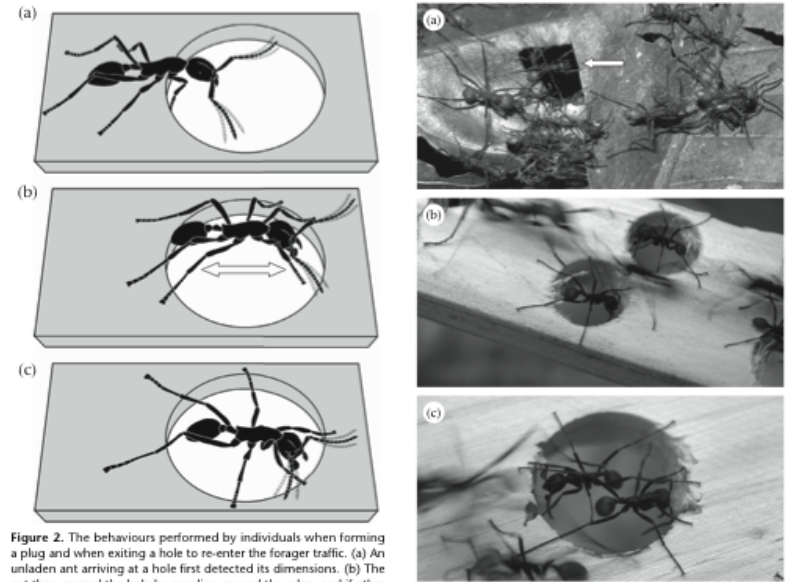
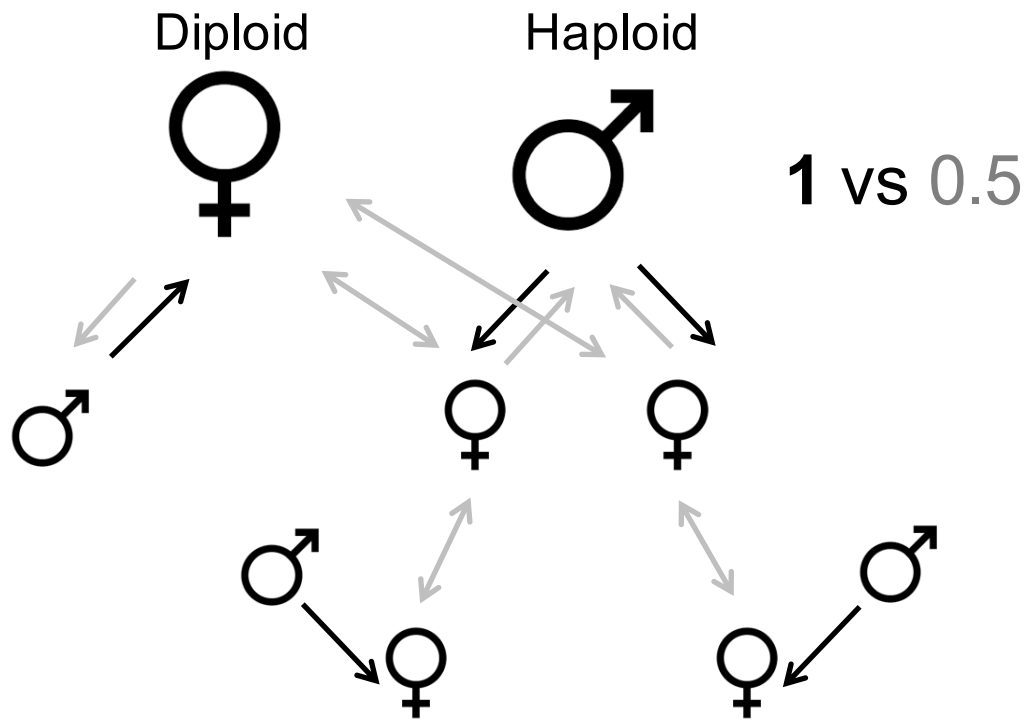


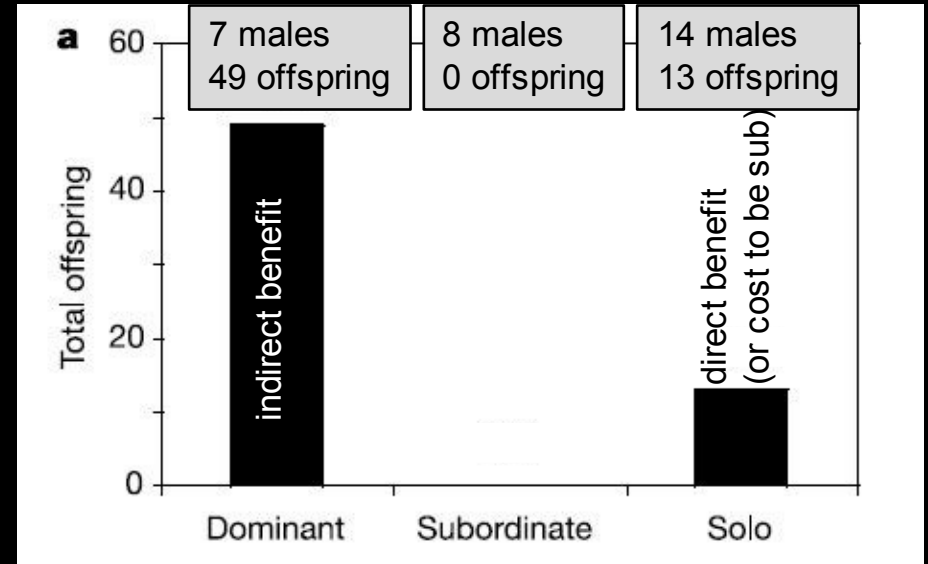
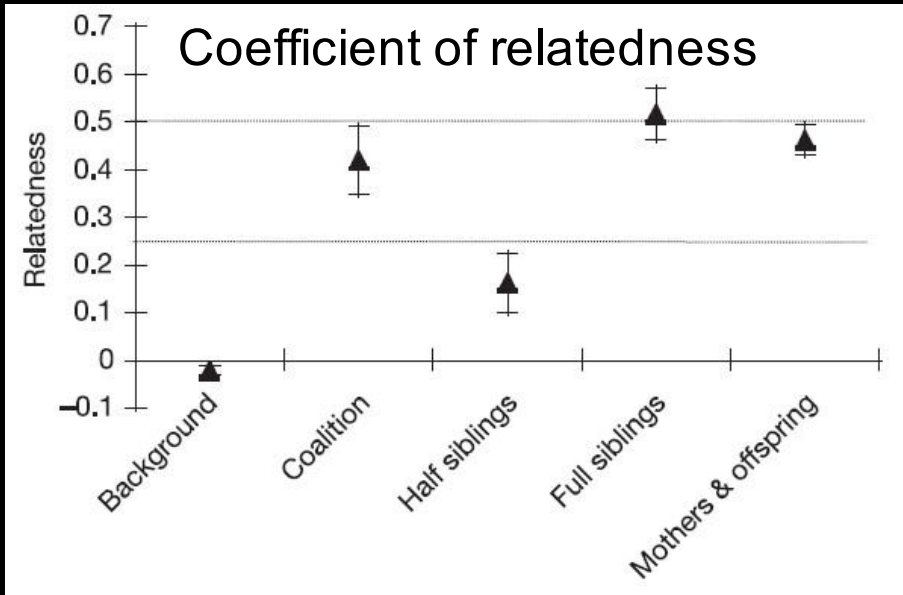
Figure 2. The behaviours performed by individuals when forming a plug and when exiting a hole to re-enter the forager traffic. (a) An unladen ant arriving at a hole first detected its dimensions. (b) The ant then crossed the hole by crawling around the edge, and if other

### Shared gene proportions in haplo-diploid sex-determination system relationships

Sex	Daughter	Son	Mother	Father	Full Sister	Full Brother
Female	1/2	1/2	1/2	1/2	3/4	1/4
Male	1	N/A	1	N/A	1/2	1/2







www.alamy.com - BFGMX9

### Kin selection and cooperative courtship in wild turkeys

Alan H. Krakauer

Nature 434, 69-72 (03 March 2005) | Download Citation

Table 1 Calculation of Hamilton's rule,  $rB - C < 0$

Variable	Description	Calculation	Value*
$r$	Coefficient of relatedness	Mean pairwise relatedness of subordinates to their dominant display partner	0.42
$B$ †	Benefit to dominant	(No. of offspring per dominant male) - (no. of offspring per solo male)	6.1 (9.0)
$C$ †	Cost to subordinate	(No. of offspring per solo male) - (no. of offspring per subordinate male)	0.9 (2.3)
	Net benefit†	$rB - C$	+1.7 (1.5)

Dominant, solo and subordinate refer to dominant coalition males, solitary non-cooperating males and subordinate male helpers, respectively.

\*Values in parentheses exclude non-reproducing males from mean fitness calculations.

† In units of offspring per male.



Alarm calls appear Altruistic?

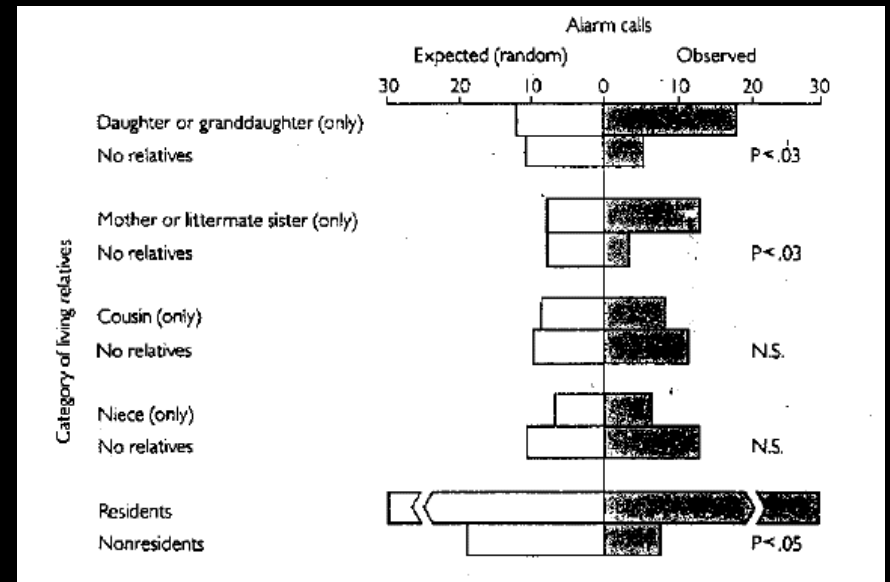


Figure 6-4

Alarm calls as a function of the presence or absence of close relatives. The graph shows the expected number of alarm calls (based on their frequency in the population) and the observed number of calls for adult female Belding's ground squirrels, within a given category of relatives alive or no relatives alive. The final comparison is between resident and newly arrived immigrants. N.S. means "not significant." Note that the presence of cousins and

Provide three alternative hypotheses that could explain this behavior could evolve through Natural Selection.

# Green Beard

1 causes a phenotype

2 recognizes that phenotype

3 differential treatment

(pleiotropic)



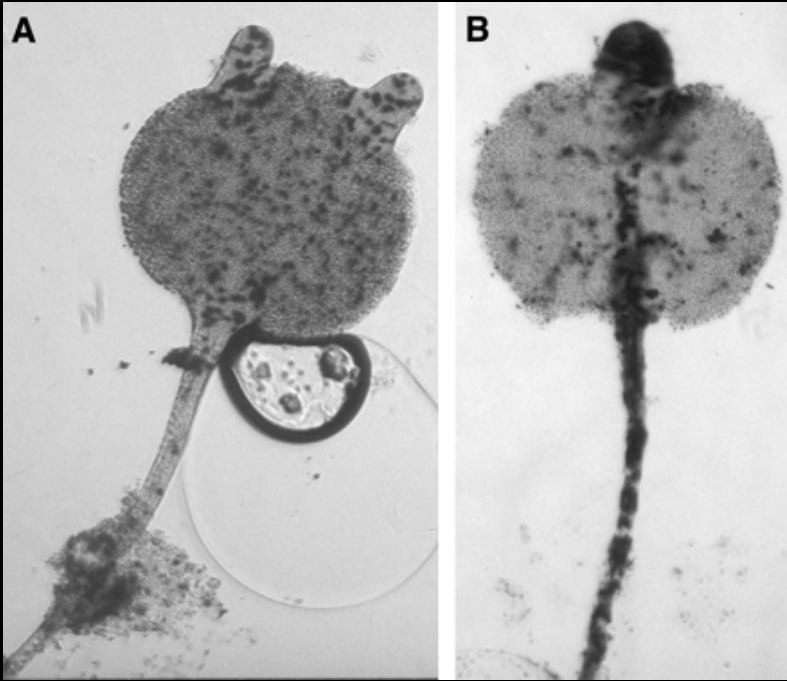
Selfish Gene Hypothesis



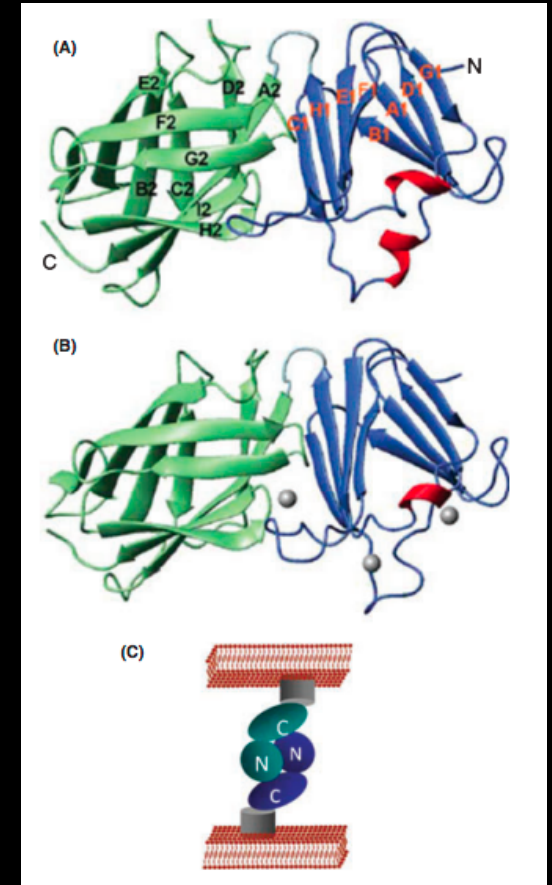
<https://youtu.be/bkVhLJLG7ug>







csA



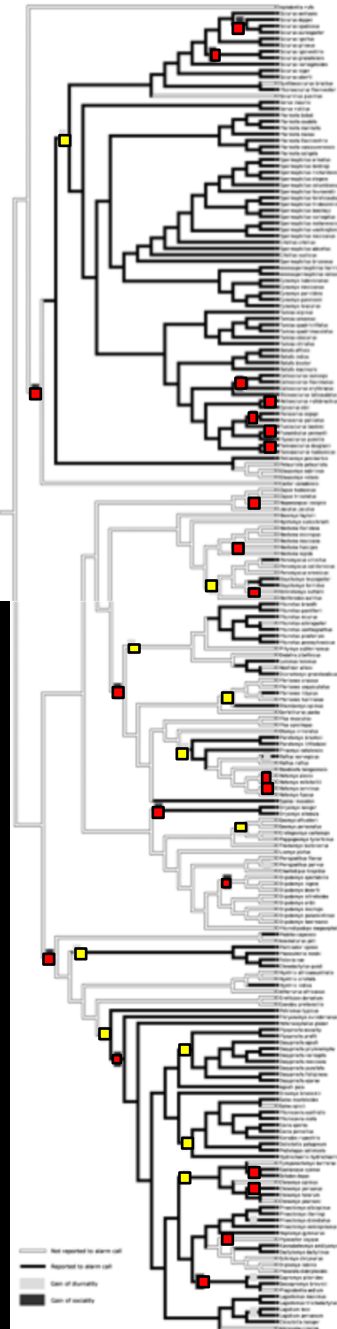
*Dictyostelium discoideum*

What sort of gene could this be?



Calling  
Not calling

sociality  
diurnality



“If calling evolved to have a conspecific alarming function then we would expect that the evolution of sociality would precede the evolution of calling”

“If calling evolved to be directed toward predators, we assumed that individuals would do so when they were relatively safe (not in the dark where it is difficult to assess predation risk)... and evolution of diurnality would precede the evolution of calling”



The answer to a phylogenetic question may differ from the answer to a question about Adaptive Value.

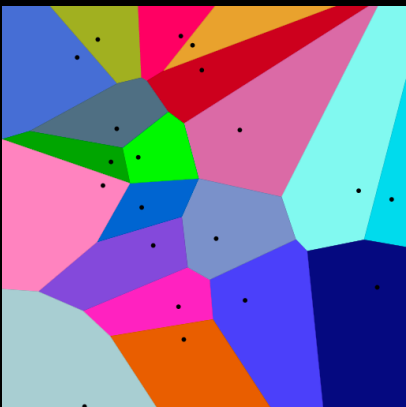
Shelly and Blumstein 2005 marmot calls





**Selfish Herd**

**Mutualism**



Voronoi Diagram







# Prisoner's Dilemma

$T > R > P > S$   
 $(T + S) / 2 < R$

-2 years for the minor crime  
 -8 years for the major crime

	Cooperate	Defect
Cooperate	<b>Reward</b> You both keep quiet You both get <b>-2</b> years	<b>Sucker</b> You keep quiet Partner gives you up You get <b>-10</b> years
Defect	<b>Temptation</b> You defect give up your partner Your partner is quiet You get out free <b>0</b>	<b>Punishment</b> You both give up the other. And both get Charged major crime You both get <b>-8</b> years

<http://bio150.chass.utoronto.ca/pdgame/index.html>



W.D. Hamilton

**The Evolution of Cooperation**  
 Robert Axelrod; William D. Hamilton  
*Science*, New Series, Vol. 211, No. 4489. (Mar. 27, 1981)



Robert Axelrod





# Prisoner's Dilemma

$$T > R > P > S$$
$$(T + S) / 2 < R$$

	Cooperate	Defect
Cooperate	R 2	S 0
Defect	T 3	P 1

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<http://sites.sinauer.com/animalcommunication2e/chapter13.01.html>



Robert Axelrod

ALTERNATE: Alternate between C and D, starting with a C.

ALWAYS COOPERATE: always play C, (Also known as sucker).

ALWAYS DEFECT: always play D. (Also known as cheat).

GRUDGER: Start with C and continue until partner plays D. D for the rest of the game.

RANDOM: The player chooses either C or D with equal probability.

**TIT FOR TAT: Start with C and plays whatever its partner did in the previous move**

NAÏVE PROBER: Start with C and then play whatever its partner plays previously.

However, randomly play D.

TIT FOR TWO TATS: Start with 2 Cs. If partner plays 2 Ds then D, otherwise C.

TWO TITS FOR TAT: Starts with C, if partner plays D then D for 2 moves.

Otherwise C

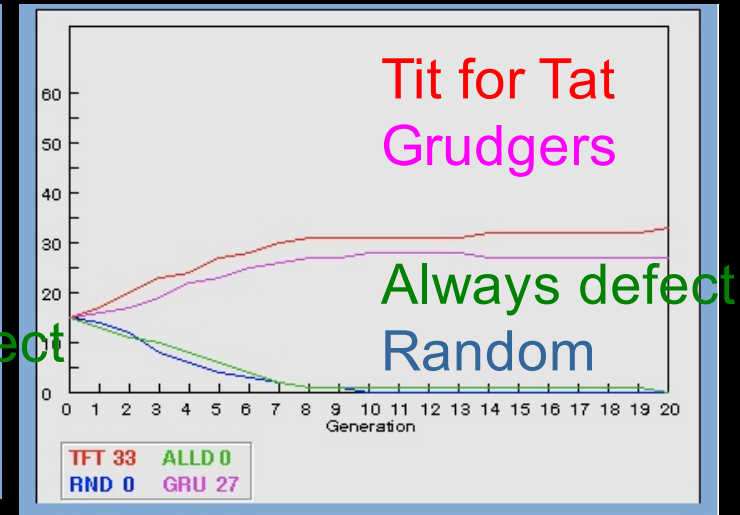
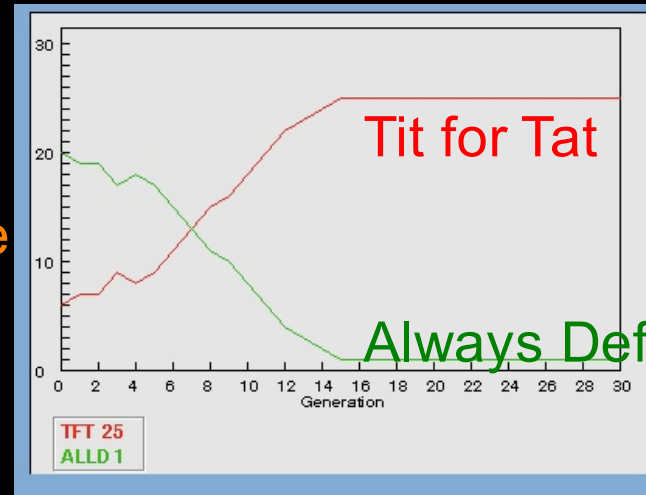
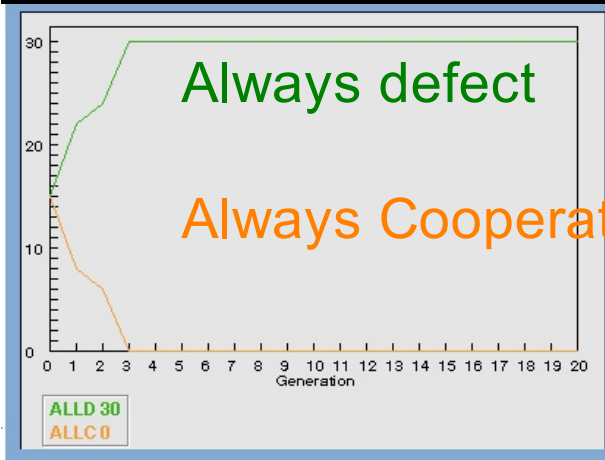
REMOURSEFUL PROBER: Start with C and play whatever partner played previously.

However, randomly play D, allow one free hit if partner's D was in response to the random D

## Strategies for Prisoner's Dilemma

	Cooperate	Defect
Cooperate	R 2	S 0
Defect	T 3	P 1

# ESS depends upon participating strategies



But both are stable

stopped here in 2018

<http://bio150.chass.utoronto.ca/pdgame/index.html>

<http://ncase.me/trust/>