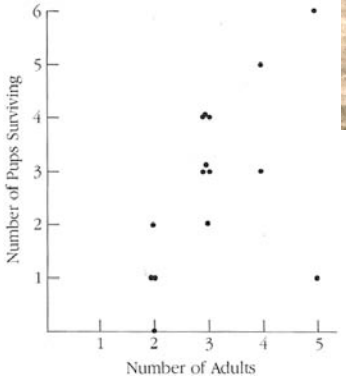
"One lifetime, nine lifetimes are not long enough for the task of blocking every cranny through which calamity may enter…… A life spent, however victoriously, in securing the necessities of life is no more than an elaborate furnishing and decoration of apartments for the reception of a guest who is never to come. Our business here is not to live, but to live happily."

A.E. Housman, 1892



Black-backed jackal
(Canis mesomelas)

Evolution of Social Behavior: Kin Selection & Sociobiology

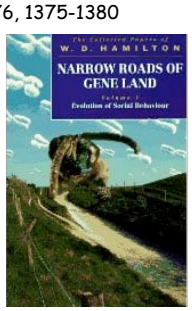
Goal: Why does altruism exist in nature?

Defn Altruism: behavior that decreases the fitness of the actor and increases the fitness of the recipient

"... special difficulty...."

Inclusive Fitness Concept

- The evolution of altruistic behavior (1963) The American Naturalist
- The genetical evolution of social behaviour I & II (1964) Journal of Theoretical Biology
- Inclusive Fitness Theory from Darwin to Hamilton (2007) LA Dugatin Genetics 176, 1375-1380



Inclusive Fitness Concept

Fitness = direct + indirect

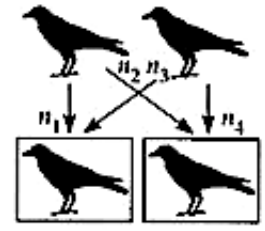
Hamilton's Rule:
altruistic behavior can spread when

$$br - c > 0$$

where
- b benefit to the recipient
- r coefficient of relationship
- c cost to the actor

William D. Hamilton
1964

Calculating coefficients of relatedness… r



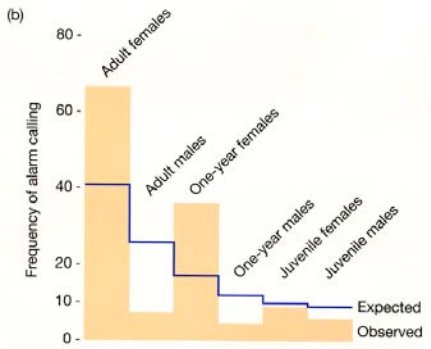
$r = (0.5)^2 + (0.5)^2$

$r = 0.5$

Siblings

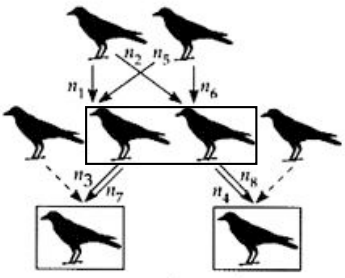
Sewall Wright

Alarm calling in Ground Squirrels….



Spermophilus beldingii

Sherman 1977



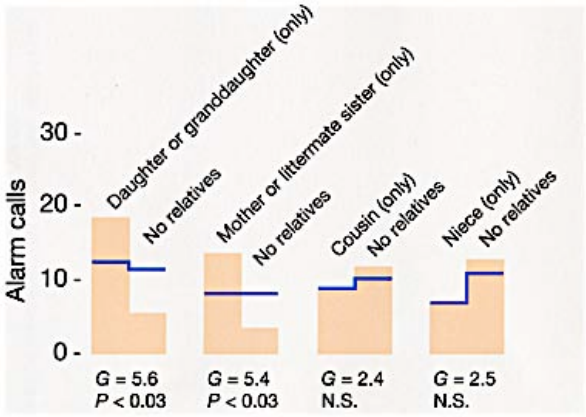
$r = (0.5)^4 + (0.5)^4$

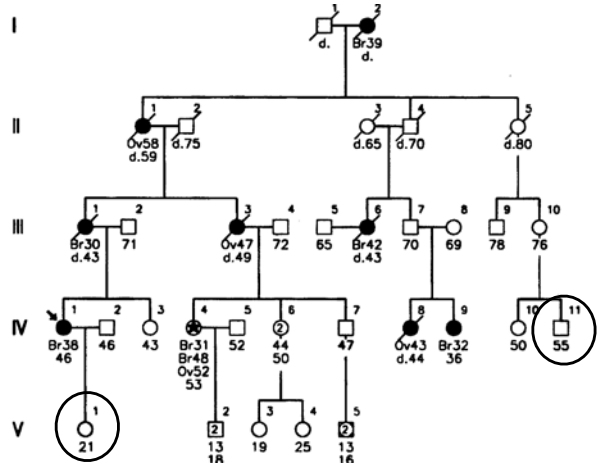
$r = 0.125$

Full cousins

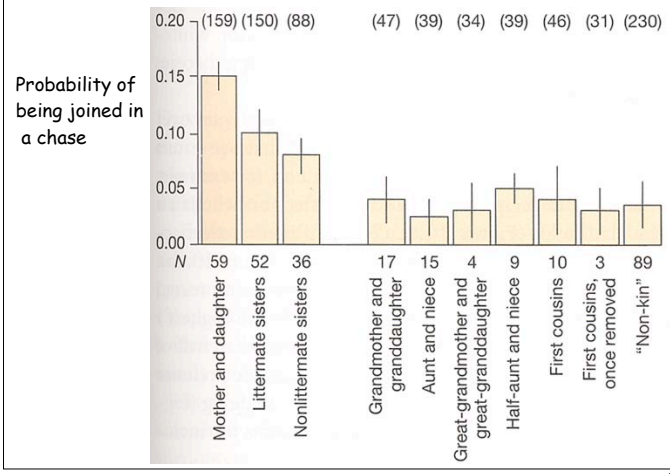
Parent - Offspring	1/2
Full Siblings	1/2
Half Sibs	1/4
Grandparents - G'child	1/4
Aunt/uncle - Niece/nephew	1/4
First cousins	1/8

- call when close kin are near





- cooperate in chasing trespassers



Communal breeding in birds & mammals...

White-fronted Bee-eater (Emlen et al, 1988)

- r largely determines whether a non-breeder will help
- individuals actively decide to help the closest r available in the clan

No helpers: >50% die before fledging
Helpers: add av. 0.47 young each

Kin Recognition

- direct mechanism e.g. phenotype matching
- indirect e.g. kin-structured population

Of Mice & Men….

Mus musculus

- communal nesting
- discriminate full & half sibs from MHC-encoded glycoproteins in urine

- F choose mates with different MHC genotypes
- F nest with females of similar MHC genotype
- some data suggest preference is learned, not innate

Humans....
males wore T-shirts 2 days
females evaluate 7 (3 similar MHC, 3 dissimilar MHC, 1 fresh)

Klaus Wedekind

Results:
- were more likely to prefer scent from dissimilar MHC
- preferences reversed with birth control pills

Extreme altruism…. Eusociality

- reproductive division of labor (sterile castes)
- cooperative care of young
- offspring help parents reproduce

How many times has eusociality evolved?

1. Hymenoptera….. ants, bees, wasps
- sterile f workers help queen
- haplodiploidy (m haploid; f diploid)

Compare r of sisters…..

Diploid	Haplodiploid	
Full siblings	Female/Sister	Female/Brother
$r = (0.5)^{2+}(0.5)^2 = 0.5$	$r = (0.5)(0.5) + (0.5)(1.0) = 0.75$	$r = (0.5)(0.5) = 0.25$

- full sisters in haplodiploid spp >> r than sibs in diploid spp
- partially explains freq. evolution of altruism in hymenoptera

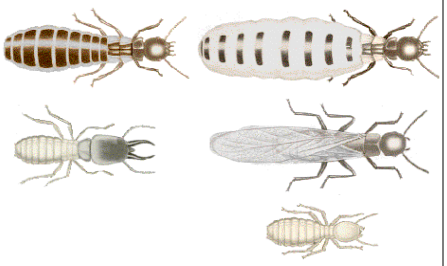
Measure <u>actual</u> r

- < 0.75 & often << 0.50
- single queen mates multiply >> sisters are really half sibs
- multiple queens in colony

Haplodiploidy does not invariably lead to high r

2. Termites & mammals….

- Similar colony structure with extreme specializations (e.g. warriors, workers, single queen)
- Regular diploid genetic system



Alternative H_o for eusociality….

1. Kin Selection: haplodiploidy
2. Parental Manipulation: queens suppress daughters reproduction
3. Mutualism: workers may obtain higher reproductive success by helping rather than founding a new nest because of cryptic reproduction

- colonial (70-80)
- dig cooperatively
- hairless

- 1 reproductive female & 2-3 reproductive males
- Ontogenetic caste system..
  care for young > dig tunnels > defend colony
- Highly inbred (r=0.81) (parent/offspring or sib/sib mating)

Altruism without kin or inbreeding? ….
'True altruism'

Rule:

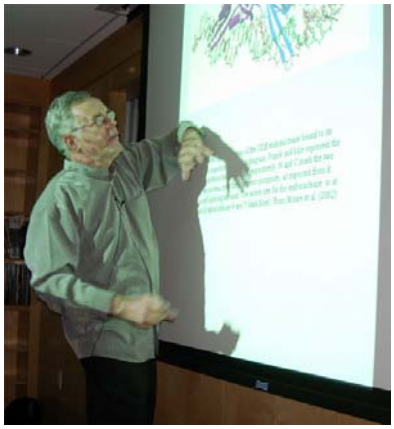
offspring =
1/2 # mammaries

But…
av 12 mammae
up to 28 pups

Human Altruism

e.g: Blood sharing in vampire bats
- starve in 3 nights

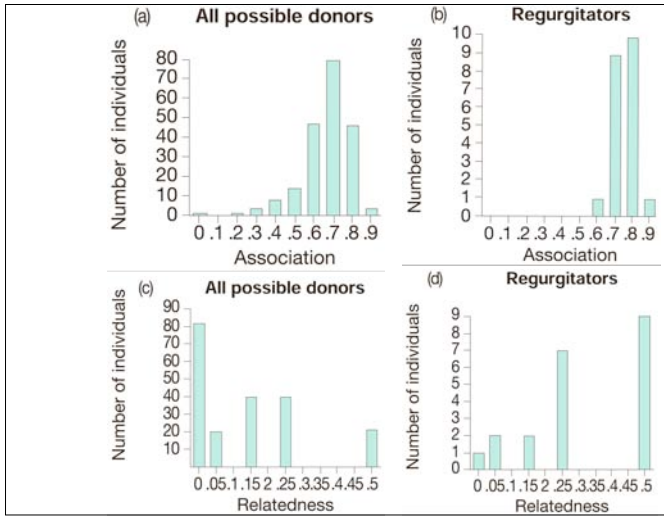
'True altruism'



Robert Trivers 1971

•How did it arise?

•How to avoid cheaters?



- p of regurgitation depends on r & association
- reciprocal

The Prisoner's Dilemma: Game theory approach to the evolution of cooperation

The Prisoner's dilemma: Game theory approach to the evolution of cooperation

		Player B's action	
		C Cooperation	**D Defection**
Player A's action	**C Cooperation**	R (reward for cooperation—both receive light sentences)	S (sucker gets longer sentence if partner defects)
	D Defection	T (temptation—reduced sentence for defector)	P (punishment for mutual defection—both receive intermediate sentences)

For player A: **T > R > P > S**

Axelrod & Hamilton (1981)

'Tit-for-Tat' is an ESS (Evolutionarily Stable Strategy)

Rules of the game….

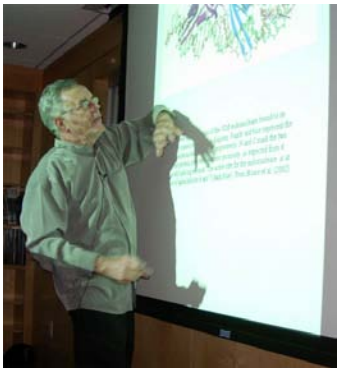
- never be first to defect
- immediate retaliation for defection
- willing to cooperate again after just one retaliation for a defection

'True altruism'

Reciprocal altruism...

Individual interacts repeatedly with the same individuals

- many opportunities for altruism
- potential altruists interact in symmetrical situations



Robert Trivers 1971