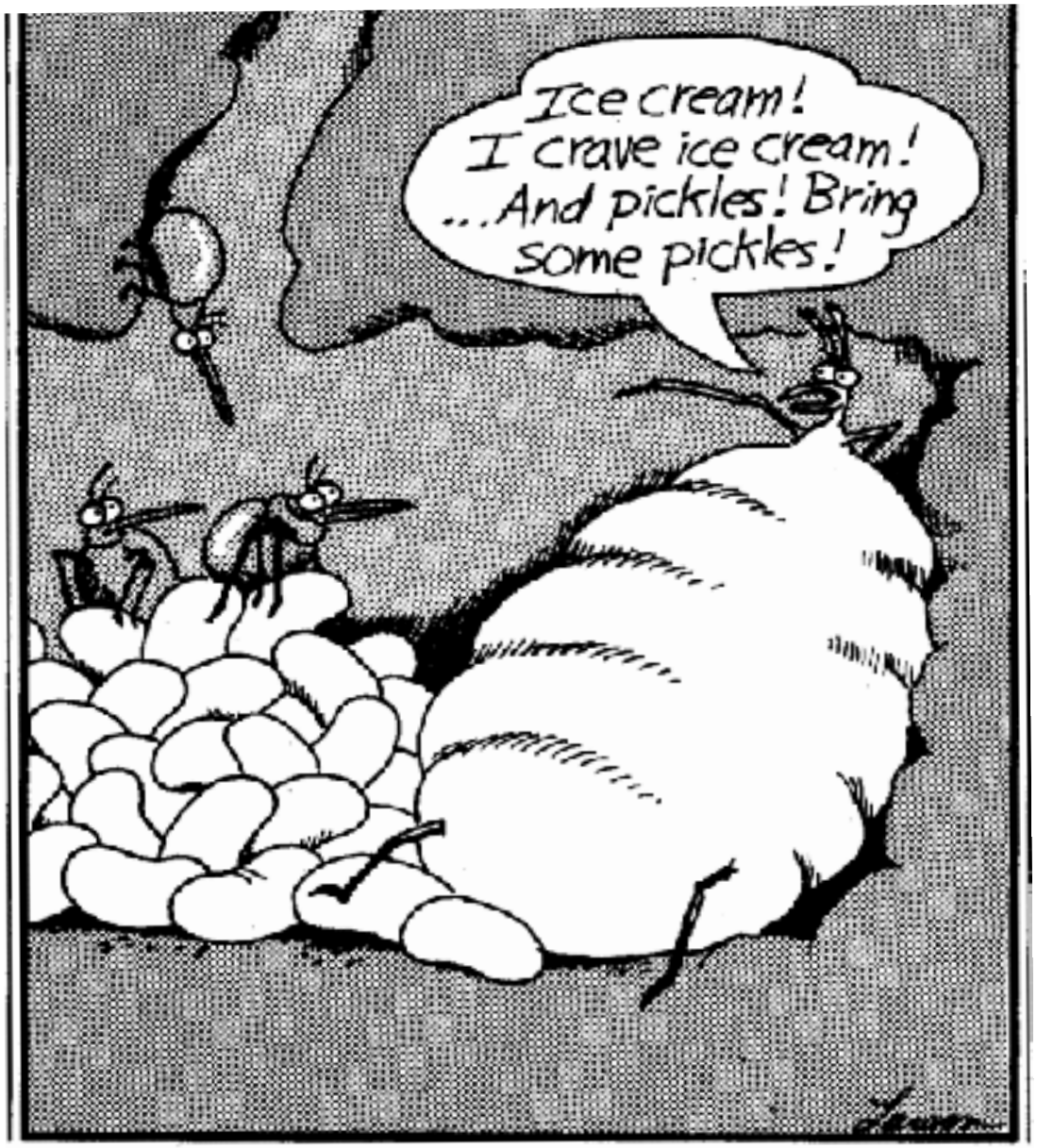
Social behavior, part 2



The termite queen in her egg chamber

Types of social interactions

Change in actor fitness	Change in recipient fitness: +	Change in recipient fitness: -
+	mutualism	selfishness
-	altruism	spite

Mutualism

- Inter- or intra-specific interaction in which both interactors benefit immediately
  - – Examples
    - Seed dispersal/Pollination
    - Foraging/Grooming
    - Protection

Types of social interactions

Change in actor fitness \ Change in recipient fitness	+	-
+	mutualism	selfishness
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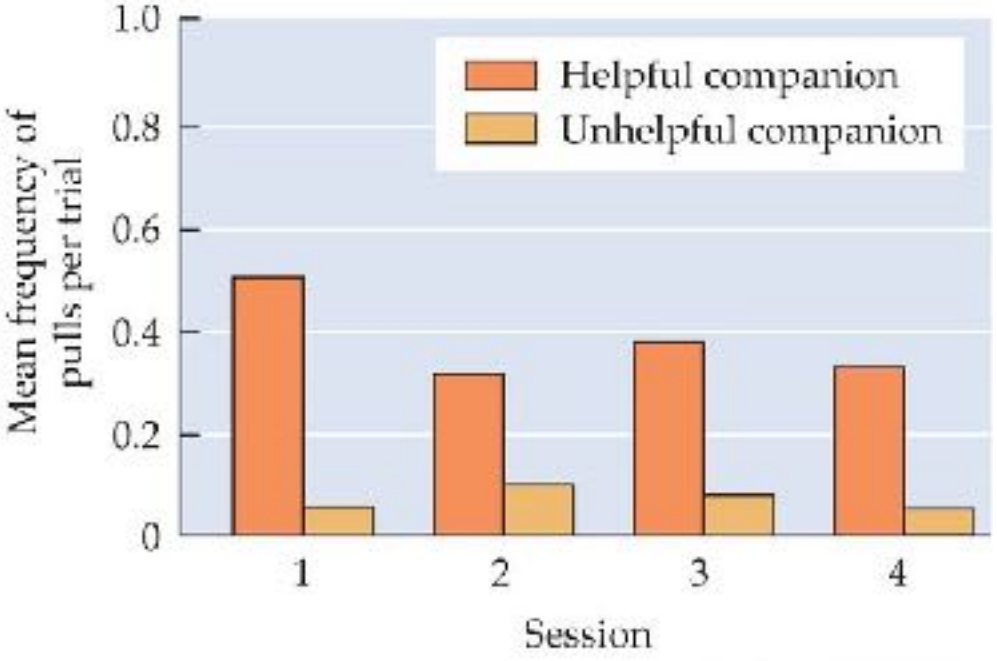
Explanation is either: 1) reciprocal altruism or 2) kin selection

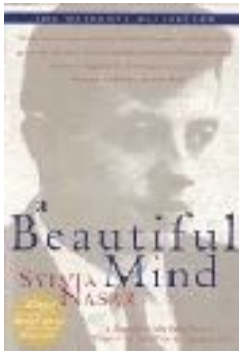
Reciprocal altruism

- Cotton-top tamarins
  - Positioning food to help a companion grab it
    - Occurred much more often when focal tamarin was matched with a tamarin (unrelated) who helped in the past



Game theory

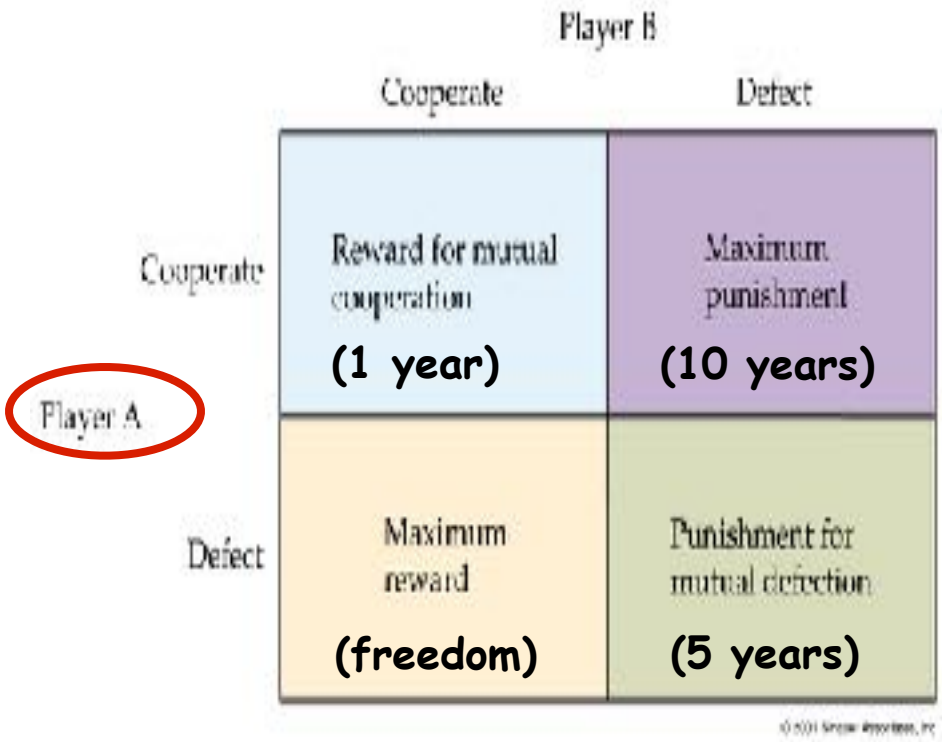
- General question: what is optimal behavior in a situation where there isn't a single "best" thing to do
  - Depends on what others do (or are *likely* to do)
- John Nash
  - Nobel prize (Economics) for contributions to game theory
  - "Nash equilibrium"
    - Stable equilibrium allowing two strategies in a game to coexist



- Game theory uses models to predict phenomena, and can determine which variables underly the decision rules
  - Makes predictions about which social behaviors will be stable over evolutionary time (ESS = evolutionarily stable strategies)
    - » ESS = a set of behaviors that is resistant to "invasion" by any mutant alternatives ***if*** *everyone's already doing the current ESS*

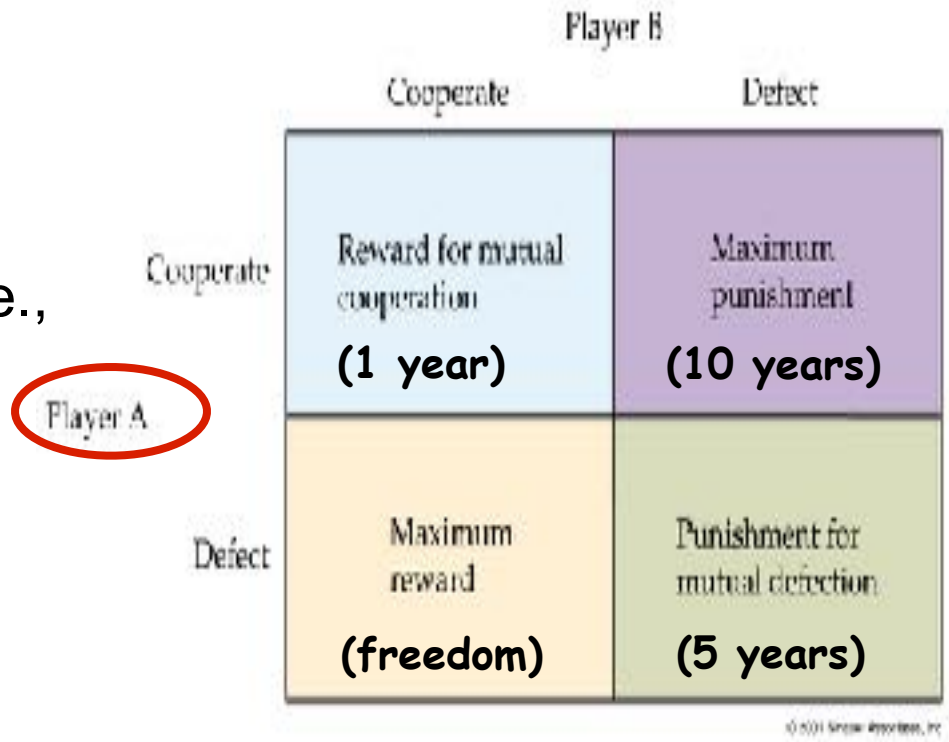
Reciprocal altruism

- Using game theory to model cooperation



Reciprocal altruism

- Using game theory to model cooperation
  - Simple prisoner's dilemma computes that reciprocal altruism shouldn't evolve
    - Always better to defect (i.e., cheaters are favored; reciprocity not an ESS)



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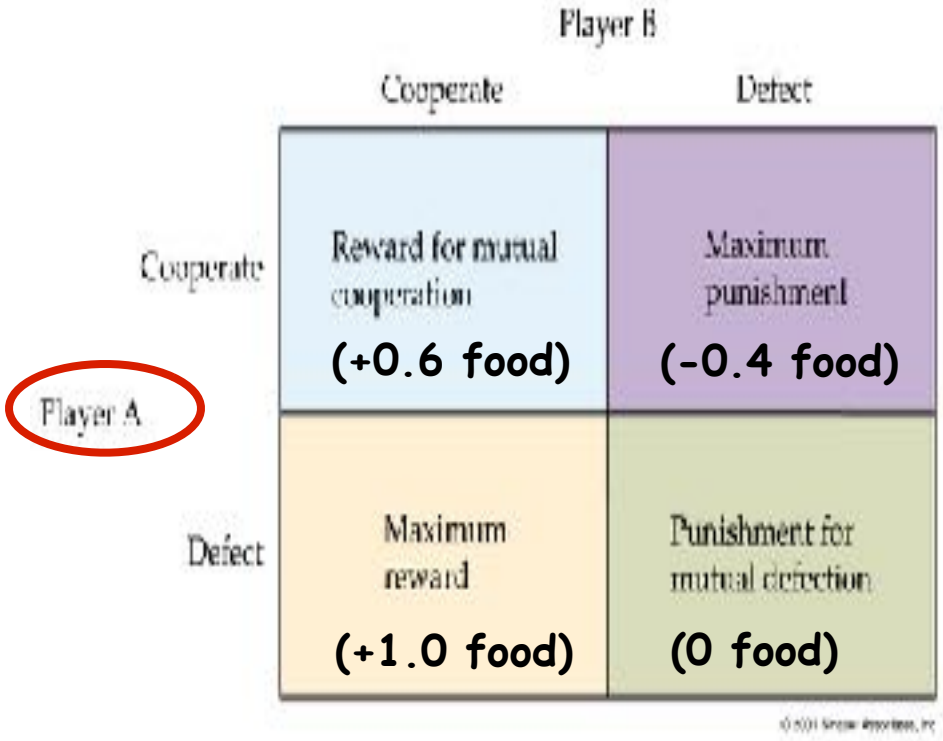
energy and risk of sharing drops food value by 0.4

Player A \ Player B	Cooperate	Defect
Cooperate	Reward for mutual cooperation (+0.6 food)	Maximum punishment (-0.4 food)
Defect	Maximum reward (+1.0 food)	Punishment for mutual defection (0 food)

Reciprocal altruism

energy and risk of sharing drops food value by 0.4

- How to model reciprocity
  - "tit-for-tat" can be an ESS:
    - Rule: always start as cooperator, and then do what other did
      - » Rewards from back and forth cooperation ADD UP, exceeding short-term payoff from a single defection
      - » ESS when there are multiple interactions with same individuals AND individual recognition



Reciprocal altruism

- Allo-feeding in vampire bats: unrelated females share blood meals with unsuccessful foragers
  - Reciprocity can evolve because:
    - 1) Many chances for repeated interaction
    - 2) Individual recognition, so can punish cheaters (withhold blood)
    - 3) Cost to donor low (little blood given), but VERY beneficial to the starving receiver (can survive until can suck blood tomorrow)

https://ncase.me/trust/

Types of social interactions

Change in actor fitness	Change in recipient fitness: +	Change in recipient fitness: -
+	mutualism	selfishness
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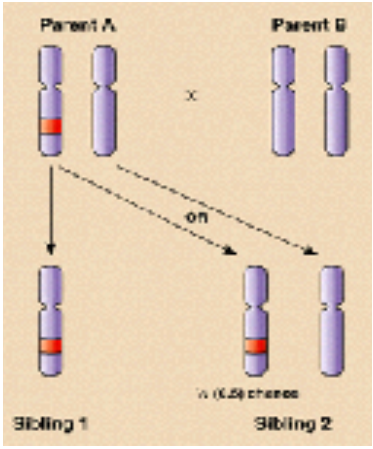
Either reciprocal altruism or kin selection

Inclusive fitness

- Fitness refers to number of surviving offspring and other descendant relatives (grandchildren, etc.)
  - Each offspring contains only half of parent's genes
    - Siblings also share half their genes, *because they had the same parents. The*se genes are identical by descent (IBD)



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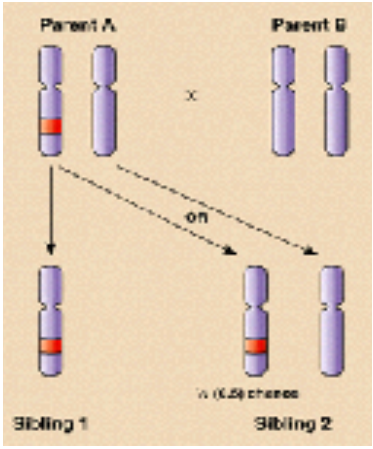
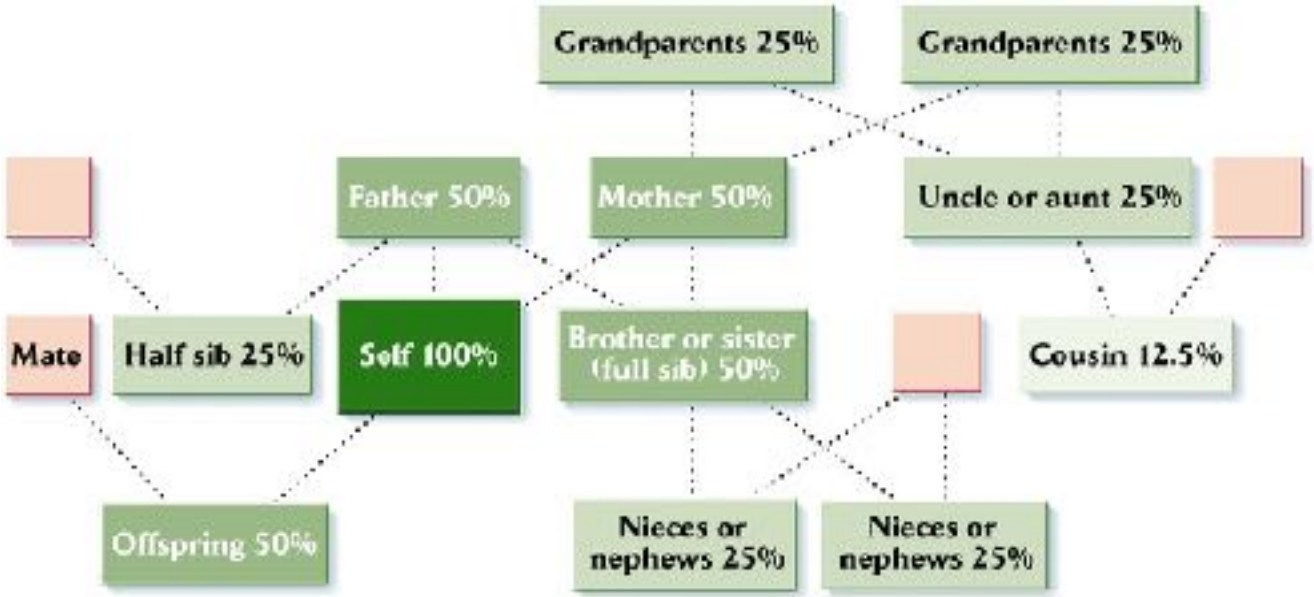


- What really matters is inclusive fitness
  - Direct fitness = via reproduction (own kids)
  - Indirect fitness = via non-descendant relatives
    - Direct + Indirect = **Inclusive Fitness**
      - Doing something that causes others to produce non-descendant relatives is (genetically) just like reproducing: helping mom & dad to make an "extra" sibling is like having a kid of your own

Calculating relatedness

- It's not just about siblings and offspring…
  - All relatives that share common ancestor(s) have copies of genes that are Identical by Descent (IBD)
  - Can calculate relatedness (*r*) for any category of relative
    - Probability that a particular gene is IBD in both individuals or, proportion of IBD genes shared between 2 individuals



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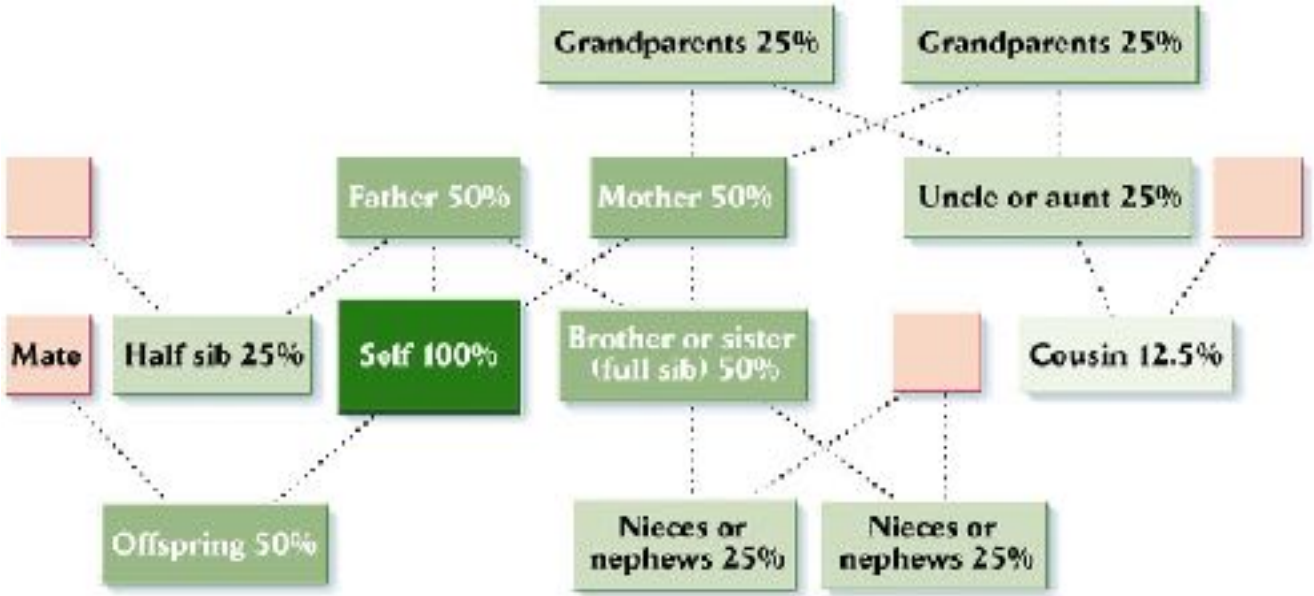


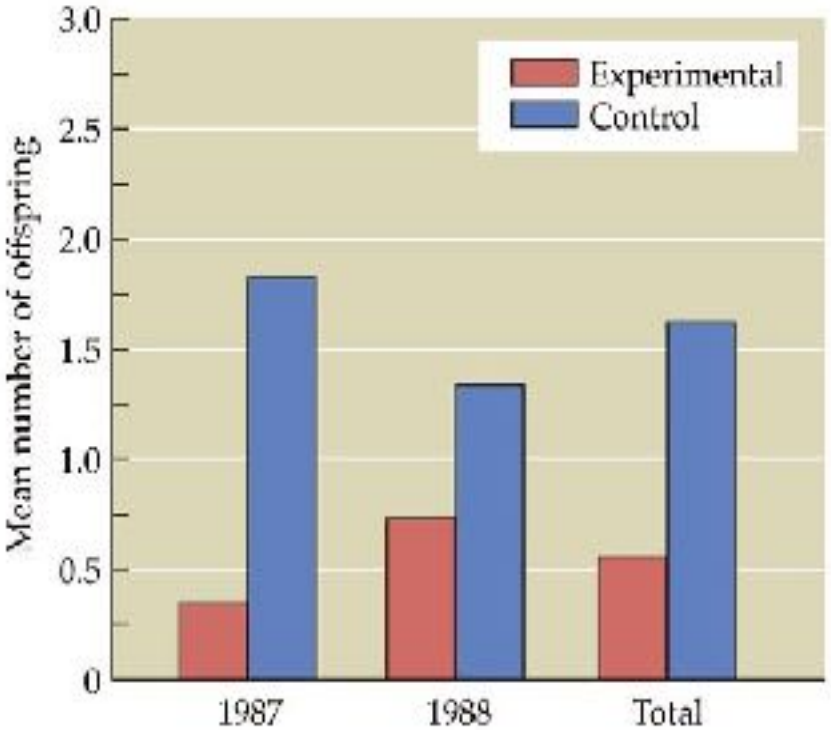
"I would give up my life for 2 brothers or ?? cousins"

Florida scrub jay example

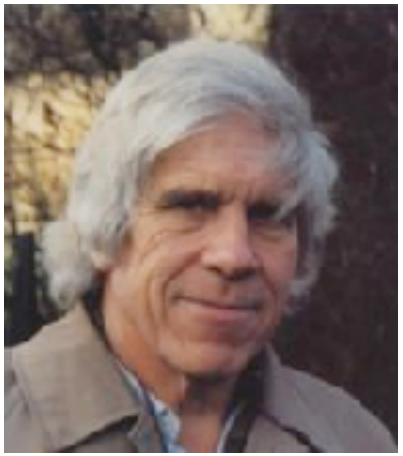
- Only 1 nest (and 1 breeding pair) in group
  - Non-breeding helpers feed young, fight off predators, defend territory
  - Why do helpers stay and forego their own reproduction?
    - No place to go: all good habitat filled, so have to wait
    - Next best thing to own reproduction: help raise ‘extra’ kin

Effects of helpers on fitness

- Helpers really do help in raising more siblings
  - when removed helpers: do not produce as many young



Hamilton's Rule



- Hamilton's Rule (i.e., how kin selection works)
  - Genes influencing behavior increase if …

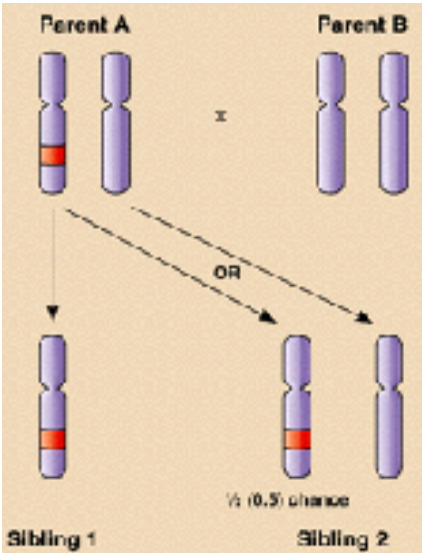
$$rB-C > 0$$

or: $rB > C$

- B = benefit to the recipient
- C = cost to the altruist
- r = coefficient of relatedness

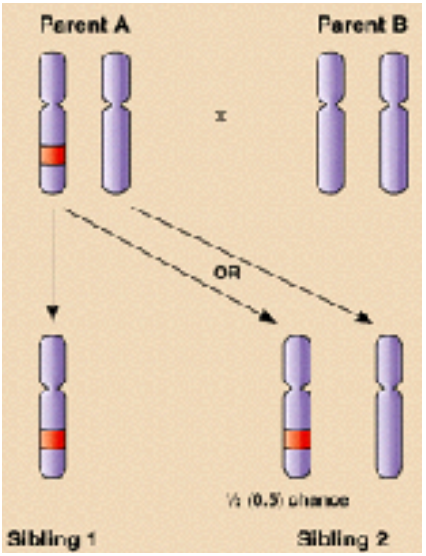
Kinship calculations

- (r) relatedness:
  - Probability that alleles in one individual are shared, due to common ancestry, in another individual
- According to Hamilton's Rule, would you lay down your life for one sister?
  - Remember it will be favored if rB-C>0



Kinship calculations

- (r) relatedness:
  - Probability that alleles in one individual are shared, due to common ancestry, in another individual
- According to Hamilton's Rule, would you lay down your life for one sister?
  - Remember it will be favored if rB-C>0
    - Answer is 'No': B=1, C=1 and r=0.5
      - 0.5(1)-1 > 0 (not true)
        - requires B=3 (three sisters) for fitness to be greater than zero.
        - or once altruism evolves in species, altruism alleles can be maintained if B=2 (fitness equivalent)



Hamilton's Rule problem

- Which behavior would be more highly favored?
  - Direct help to mother + father and enable them to rear 1 offspring that they would not have otherwise produced
  - Direct help to aunt + uncle and enable them to rear 5 offspring they would not have otherwise produced

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mother + father option

r between actor and offspring = 0.5 (full sibling)

0.5 x 1 offspring = 0.5

Hamilton's Rule problem

- Which behavior would be more highly favored?
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mother + father option		**aunt + uncle option**
r between actor and offspring = 0.5 (full sibling)		*r* between actor and offspring = 0.125 (cousins)
0.5 x 1 offspring = 0.5	<	0.125 x 5 offspring = 0.625

Increase indirect fitness more if help aunt+uncle

Testing the kin selection hypothesis

- Prediction 1:
  - Individuals should be more likely to help kin than non-kin
    - Pied Kingfishers help breeding pair more often when related

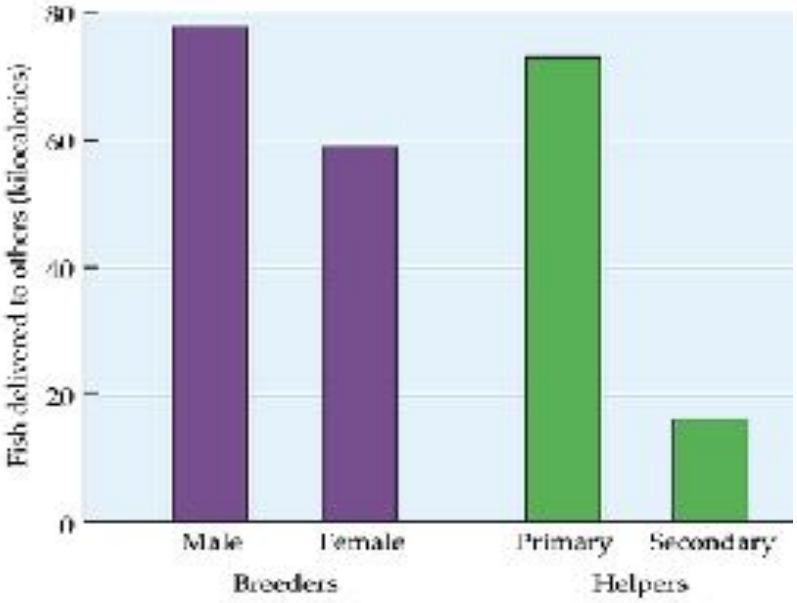

TABLE 13.3 *Calculations of inclusive fitness for male pied kingfishers*

Behavioral tactic	First year			Second year				
	y	r	f_1	o	r	s	m	f_2
Primary helper	$1.8 \times 0.32 = 0.58$			$2.5 \times 0.50 \times 0.54 \times 0.60 = 0.41$				
Secondary helper	$1.3 \times 0.00 = 0.00$			$2.5 \times 0.50 \times 0.74 \times 0.91 = 0.84$				
Delayer	$0.0 \times 0.00 = 0.00$			$2.5 \times 0.50 \times 0.70 \times 0.33 = 0.29$				

Source: Reyer [1013]

Symbols: y = extra young produced by helped parents; o = offspring produced by breeding ex-helpers and delayers; r = coefficient of relatedness between the male and y, and between the male and o; f_1 = fitness in first year (indirect fitness for the primary helper); f_2 = direct fitness in second year; s = probability of surviving into the second year; m = probability of finding a mate in the second year.

Testing the kin selection hypothesis

- Prediction 1:
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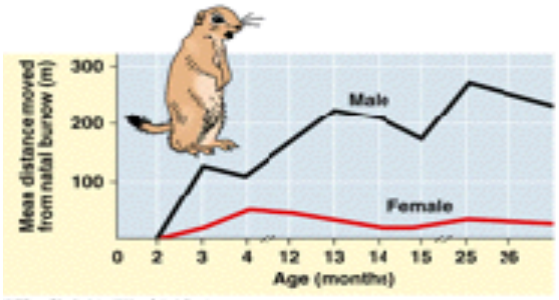
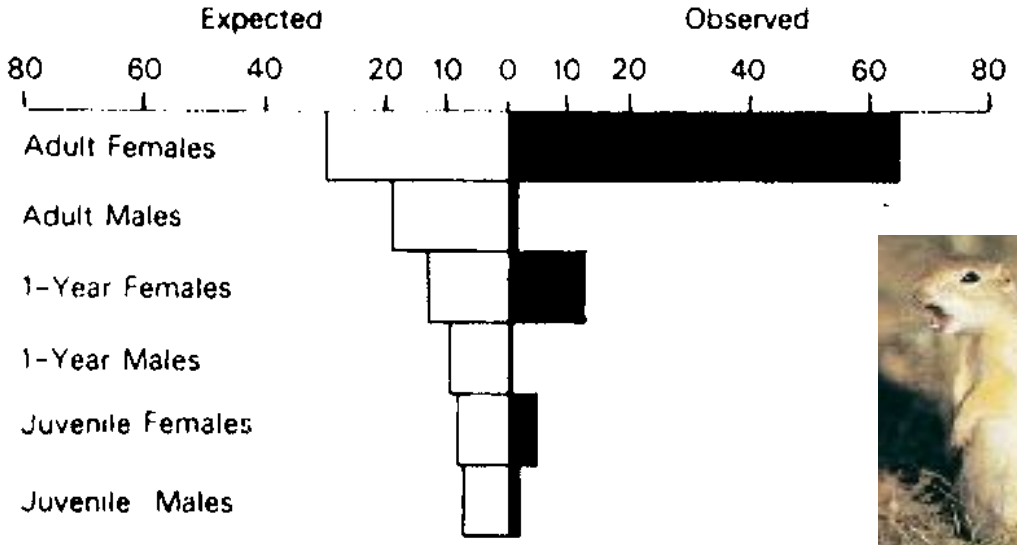
    - Belding's ground squirrels call more often with kin nearby





Testing the kin selection hypothesis

- Prediction 2:
  - Individuals should help (quantitatively) close relatives more than distant relatives
    - White-fronted bee-eaters helping, and Lion Nursing