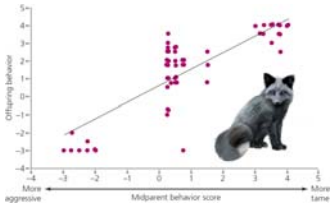
BEHAVIOR EVOLVES



- Belyaev's long term selection experiment on aggression in foxes demonstrates that behavior has a genetic basis
- QTL analysis implicates a single chromosomal region that is strongly associated with the level of aggression
- 355 genes show expression differences between aggressive and tame foxes

Figs. 16.3 & 16.4

OLDFIELD MICE PRODUCE A DISTINCTIVE BURROW

- Relatives produce burrows with short entrance and no escape tunnel
- QTL analysis revealed relatively simple genetic basis

Weber et al. 2013

- Selection produces evolutionary changes in behavior

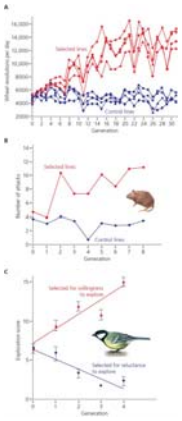
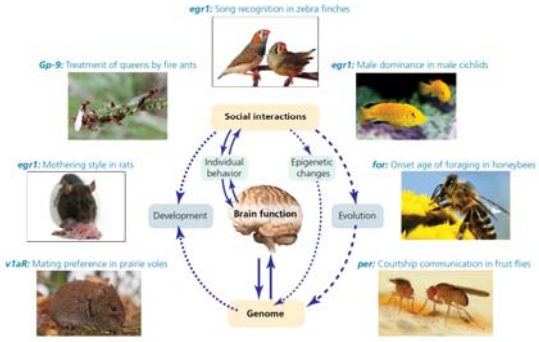
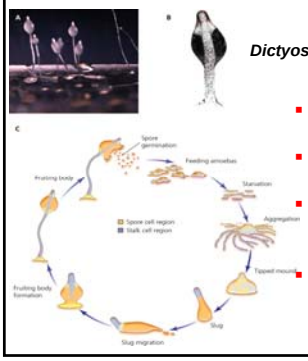


Fig. 16.6

GENES INFLUENCE BEHAVIOR

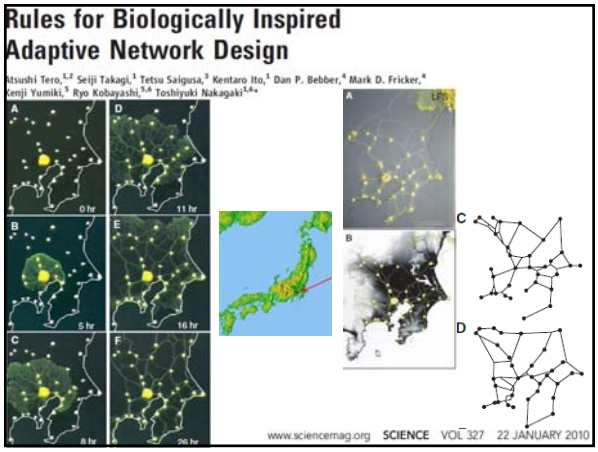


BEHAVIOR AND COOPERATION IN UNICELLULAR ORGANISMS



Dictyostelium discoides

- Amoeboid cells -- aggregate under starvation
- Form a "slug" to traverse faster
- Fruiting body with "stalk" (~20%) and "spore" (~80%) guilds
- Unicellular cooperation as precursor to multicellularity?



Rules for Biologically Inspired Adaptive Network Design

Atsushi Tero,[1,2] Seiji Takagi,[1] Tetsu Saigusa,[3] Kentaro Ito,[1] Dan P. Bebber,[4] Mark D. Fricker,[4] Kenji Yumiki,[5] Ryo Kobayashi,[5,6] Toshiyuki Nakagaki[1,6*]

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Many behaviors are involved in social interactions
- interactions between members of same species

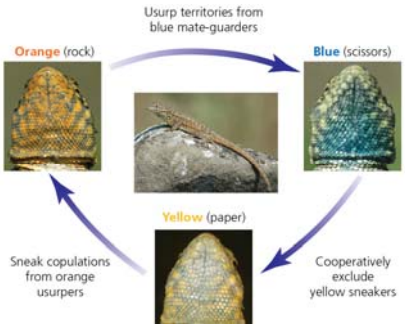
some social behavior involves cooperation

Why Cooperate When You Can Cheat?

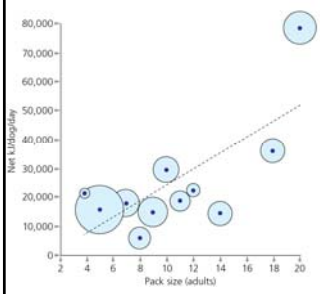
Does selection favor individuals that behave at the expense of their groups?

- **Group Selection: Groups of cooperative individuals will outcompete and displace groups of selfish individuals**
- **Evolutionary Stable Strategy: A balance of behavior(s) that, when adopted by a population of players, cannot be invaded by an alternate strategy**

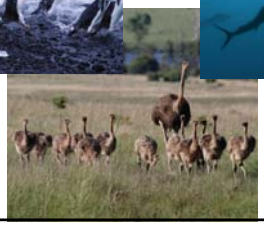
- **Game Theory: An approach to studying behavior that solves for the optimal payoff strategy, depending on the choice of other players.**



Obvious Group Advantages: Teamwork in the Wild

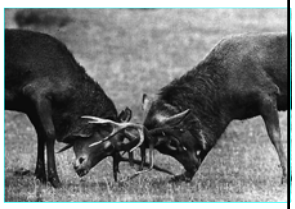


Obvious Group Advantages: Safety in Numbers



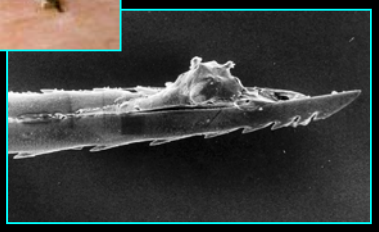
Other social behaviors are aggressive or territorial:

Gannets peck at neighbors over small territories



Stags joust over access to mates

Altruism: honey bee workers



EXPLANATIONS FOR APPARENT ALTRUISM

1. Manipulation – The donor is actually being manipulated by the recipient.
2. Individual advantage – It is actually advantageous for the donor to dispense the altruistic actions.
3. Reciprocation – The donor helps the recipient, because the recipient will reciprocate at some time in the future.
4. Kin selection – The donor is actually aiding the spread of its own genotype by helping relatives.

Sometimes selection can lead to a trait (such as a behavior) that appears to be *detrimental* to the individual expressing the trait

If organisms occur in stable kin groups, traits can evolve via kin selection

Indirect selection for alleles through an increase in the fitness of close relatives *rather than through an increase in fitness of the individual expressing the allele*

- To understand kin selection, we must adopt a *gene's - eye view:*

- Natural selection predicts only that *replicators (genes) whose effects tend to enhance the probability of replication will come to predominate.*

- Genes coding for traits that benefit close kin may *increase the probability of their own replication*, and can replace other genes.

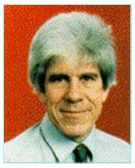
THINK ABOUT KIN SELECTION IN TERMS OF INCLUSIVE FITNESS

- **An individual's fitness (i.e., the success of its genes) is not based solely on its own reproduction, but also on all the effects it has on other individuals, weighted by their relatedness to the individual.**

Alarm-calling ground squirrel

Key concept: relatives are also likely to carry alleles for the altruistic trait

Hamilton's rule: weight fitness effects by relatedness



$$W_i = a_i - c_i + \sum r_{ij} \times b_{ij}$$

a_i = benefit to individual
c_i = cost to individual
r_{ij} = degree of relatedness
b_{ij} = amount of benefit to relatives

Natural Selection can favor the evolution of either altruism or selfishness,

$$W_i = a_i - c_i + \sum r_{ij} \times b_{ij}$$

- **Altruistic trait *will* evolve if $\Sigma rb > c$**
- **Selfish trait *will* evolve if $\Sigma rb < c$**

Question: *Would you lay down your life for your brother?*

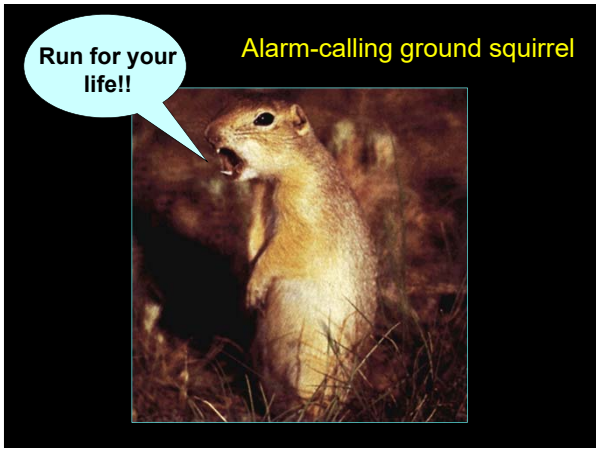
"*No*, but I would for *two* brothers or *eight* cousins"

J.B.S. Haldane

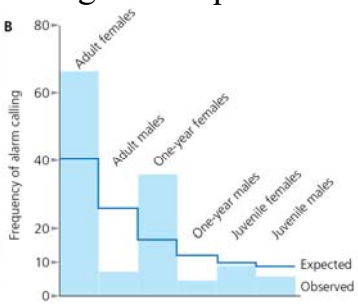
HELPING BEHAVIOR CAN EVOLVE DESPITE THE COST

KIN SELECTION AND GROUP SELECTION

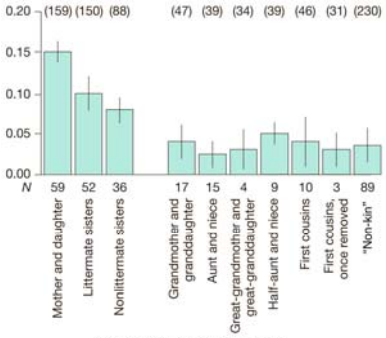
- Kin selection is sometimes viewed as a special form of group selection that works.
- But really it is a special form of individual selection. Even in social insects, there are conflicts within the group, so it is better to analyze selection with Hamilton's rule (which tallies up the net effects of genes on individuals).

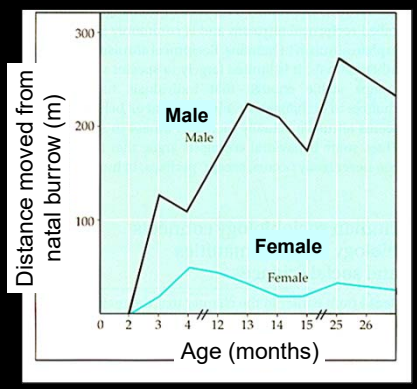


Kin selection in ground squirrels



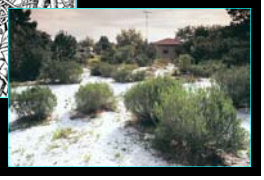
INCIDENCE OF COOPERATION IN GROUND SQUIRRELS



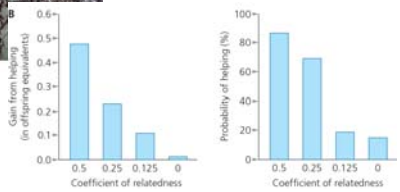


Florida scrub jays - "helpers at the nest"

- inclusive fitness *OR* direct benefit??

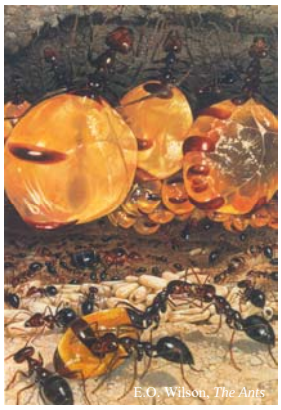


KIN SELECTION IN WHITE-FRONTED BEE-EATERS



Altruism in social insects
(termites, ants, many wasps and bees, etc.)

- Honeypot ants
- Sterility



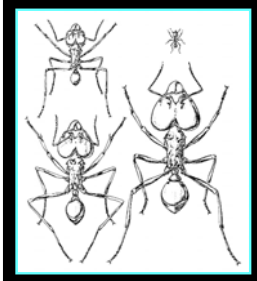
Eusociality in kin groups:

- overlapping generations
- reproductive division of labor (sterile caste)
- cooperative brood rearing

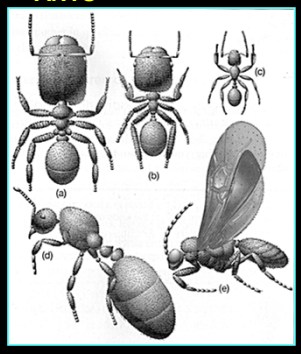
With sterile neuter insects, we have reason to believe that modifications in their structure and fertility have been slowly accumulated by natural selection, from an advantage having been thus indirectly given to the community to which they belonged over other communities of the same species.

This difficulty [of sterile insects]… disappears … when it is remembered that selection may be applied to the family, as well as to the individual

Darwin, *The Origin of Species*



- **MULTIPLE, STERILE WORKER CASTES IN ANTS**



- Eusociality (with sterile castes) *independently* evolved several times in the Hymenoptera (ants, bees, wasps)

Why??

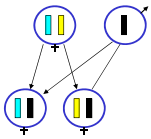
- Unusual degrees of relatedness because of *haplodiploidy* as sex-determination mechanism

Eusociality:
The extreme of social organization

- **Haplodiploidy: Mechanism of sex determination in which males are haploid and females are diploid.**

- **Females lay haploid eggs**
  - **If eggs are fertilized by haploid sperm, they become diploid females**
  - **If eggs are not fertilized, the offspring are haploid and develop into males.**

- Males develop from unfertilized eggs and are haploid.
- Females develop from fertilized eggs and are diploid.



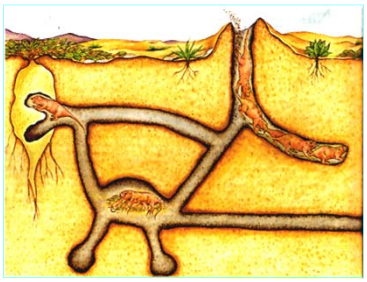
- Full sisters have a relatedness of 0.75 instead of 0.5

Females are *more* closely related to sisters than to own offspring

- But close degrees of relatedness *cannot* completely explain when eusociality evolves
- ecological reasons favor reciprocal altruism, cooperation among founding females in building a nest and caring for larvae
- must include a consideration of b and c in addition to r
- facultative reciprocal altruism in paper wasps

EUSOCIALITY IN THE NAKED MOLE RAT

- Reproduction controlled by "queen" & few large, breeding males
- 70-80 / colony in an expandable nest
- Cooperate in defense, food gathering, tunneling
- Inbreeding **(avg. r = 0.81!)**
- hot, arid climate



- Naked mole rats even have morphological castes – lumbar vertebrae lengthen with onset of reproduction in females
  - advantages for pup carrying capacity and greater hypertrophy of GI tract

Energetics reveals physiologically distinct castes in a eusocial mammal

M. Scantlebury, J. R. Speakman, M. K. Oosthuizen, T. J. Roper and N. C. Bennett

Eusociality, which occurs among mammals only in two species of African mole-rat, is characterized by division of labour between morphologically distinct 'castes'. In Damaraland mole-rats (*Cryptomys damarensis*), colony labour is divided between 'infrequent worker' and 'frequent worker' castes. Frequent workers are active year-round and together perform more than 95% of the total work of the colony, whereas infrequent workers typically perform less than 5% of the total work. Here we show that infrequent workers and queens increase their daily energy expenditure after rainfall whereas frequent workers do not. Infrequent workers are also fatter than frequent workers. We suggest that infrequent workers constitute a physiologically distinct dispersing caste, the members of which, instead of contributing to the work of the colony and helping the queen to reproduce, build up their own body reserves in preparation for dispersal and reproduction when environmental conditions are suitable.

Infrequent workers comprise as much as 40% of the colony

Nature **440**, 795-797 (6 April 2006)