Kin selection (inclusive fitness) and social behavior

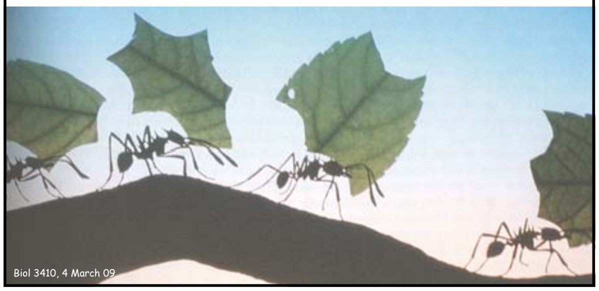
These worker ants are *sterile*, and they differ greatly from their queens and males.

Darwin was troubled by social-insect workers, because they have no fitness.

How can they evolve? If Darwin had known about genes, he would have figured it out.

The key: individuals can have *indirect* or *"vicarious"* reproductive success through *relatives*.

"Kin selection" was worked out by RA Fisher, JBS Haldane, and especially WD Hamilton.



Behavior is *social* when it affects the *fitnesses* of *other* individuals

Effect of act on fitness of *recipient*

Effect of act on fitness of *actor*		**–**	**+**	
	+	Selfishness	Cooperation	Easy to explain
	–	Spite	Altruism	Hard to explain

When the affected individuals (recipients of the behaviors) are *relatives*, selection may favor both

(1) *altruism* and

(2) *restraint from selfishness*.

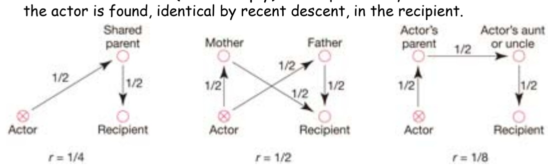
Why? Relatives are likely to carry (and hence transmit) copies of the actor's own genes, including those that induce the altruism or restraint from selfishness.

The *inclusive fitness* of a behavior is its effect on the fitness of the actor, and also on the fitnesses of the recipient(s), devalued by their coefficients of relationship to the actor.

The conditions for altruism or restraint from selfishness depend on the *coefficient of relatedness* (*r*) between actor and recipient.

r is most generally defined as the *correlation* (or regression) between the recipient's genotype and the actor's genotype.

It can also be calculated (more simply) as the probability that an allele in the actor is found, identical by recent descent, in the recipient.



r can be viewed as the degree to which *another* individual's reproduction is genetically equivalent to *mine*.

Thus Hamilton's rule for the evolution of *altruism*: $Br > C$ (B = Benefit to recipient, C = Cost to actor).

And Hamilton's rule for the evolution of *restraint from selfishness*: $B < Cr$ (B = Benefit to actor, C = Cost to recipient).

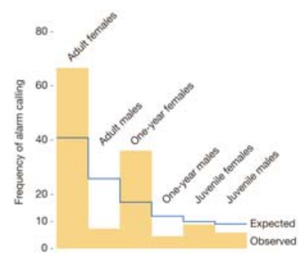
Belding's ground squirrels sometimes warn their neighbors when a predatory mammal (weasel, coyote, or badger) is near.

The caller is more likely to be killed than a non-caller.

Callers are predominantly females.

Females are more highly related to their neighbors than males are, because females tend to remain near their natal burrows, while males tend to disperse.


A female Belding's ground squirrel

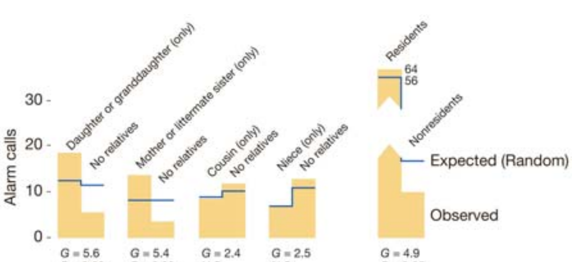


Female Belding's ground squirrels are more likely to call in response to a mammalian predator when *close* relatives are nearby.

The graphs summarize 119 cases when a mammalian predator approached a colony.

Each paired comparison represents occasions when at least one female in each category was present, but no others.

Under the null hypothesis, the "*G*" statistic is distributed as chi-square.



White-fronted bee-eaters breed in communal groups of 3-17 adults

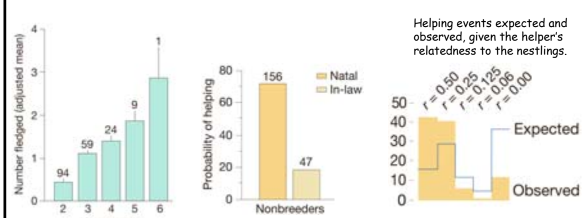
Nestling mortality is high, and larger groups fledge more young.

Individuals born in a group are more likely to help (as opposed to simply hanging out) than individuals who entered the group from outside.

And individuals are more likely to help when they are closely related to the nestlings.


A juvenile bee-eater solicits a feeding

Helping events expected and observed, given the helper's relatedness to the nestlings.



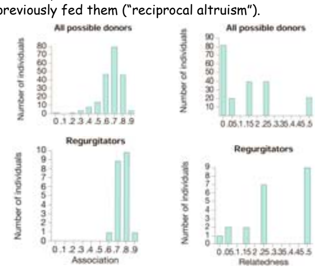
Vampire bats share blood with each other

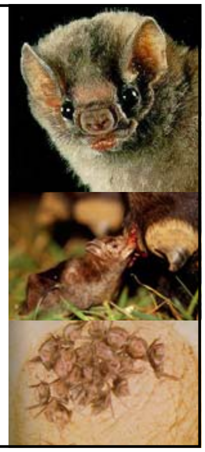
On any given night, 33% of young bats and 7% of experienced adults may fail to obtain a blood meal.

Three failures in a row may be fatal.

Gerald Wilkinson followed 200 individuals at a site in Costa Rica for nearly five years.

Individuals were much more likely to share blood with relatives, and with unrelated-roostmates that had previously fed them ("reciprocal altruism").





Coots avoid being inappropriately altruistic

Female coots (*Fulica americana*) often lay eggs in other female's nests.

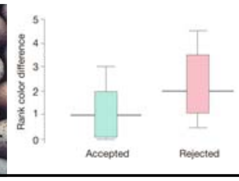
If the other female doesn't notice, this kind of intraspecific nest parasitism increases the fitness of the parasitizing female.

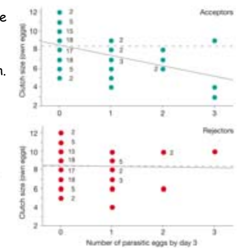
Coot eggs are highly variable in appearance, as if to help females distinguish their own eggs from others'.

Bruce Lyon followed over 400 nests in four seasons.

Different-looking parasitic eggs were more likely to be rejected than similar-looking ones.

Females with fewer than eight eggs were more likely to be parasitized than females with eight of their own.





Individuals are expected to *disagree* about the circumstances when altruism and restraint from selfishness are appropriate.

For example, your mother "wants you to be nicer to your little brother than you want to be". Why?

From your mother's (evolutionary genetic) point of view, your offspring are as valuable as your brother's, and vice versa (r = 0.25 in each case).

However, as you see it, your own offspring are worth twice as much (r = 0.5) as your brother's (r = 0.25).

Thus you are predicted to be altruistic to your brother only when B > 2C.

But your mom's fitness would be increased if you were altruistic when B > C.

And she would prefer that you refrained from being selfish when C > B.

But you don't see it that way!

This is (in theory) an irreconcilable *"conflict of interest"*.

Nice theory. But how to *test* it?

Study the sex ratios of ants!

Basic principle: the rarer sex is fitter

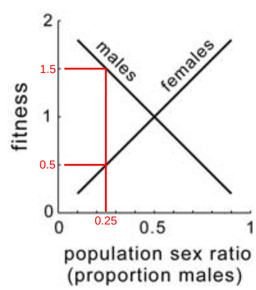
Why? Because every offspring has a mother and a father.

Thus the *total* fitness of *all* females equals the total fitness of all males.

It follows that members of the rarer sex (at mating time) are fitter. (Fitness is inversely or negatively frequency dependent.)

Thus parents that over-produce the rarer sex have more grandkids (see problem #4 in the adaptation problem set).

Note that this sex-allocation strategy is good for individuals and genes, but *not* for the species as a whole!



For example, when the sex ratio is 1:3 (M:F), the fitness ratio is 3:1.

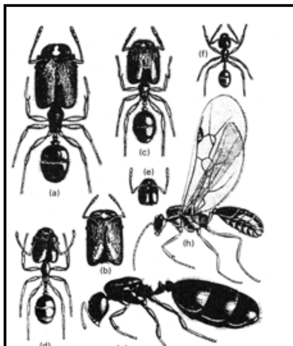


Fig. 11.4 Caste polymorphism in an advanced myrmicine ant, *Pheidole tepicana*. This famous drawing by W.M. Wheeler (1910) shows the queen (g), the male (h), and six worker subcastes, from the major worker (a), through several sizes of media workers (b–e), to the minor worker (f). Note that proportions (especially those of the head) change dramatically with size.

In ants, sisters rear their siblings

(their "virtual offspring", $r = \frac{3}{4}$).

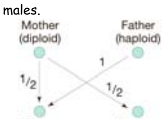
The queen is equally related to her sons and daughters (r = 0.5), but workers are three times as related to their reproductive sisters (r = 0.75) as to brothers (r = 0.25), if the queen mated only once.

Thus workers would increase their indirect fitness by investing more of the colony's resources in female than in male reproductives.

They gain equal fitness from investment in female and male reproductives when the population sex ratio (of investment) is 3:1 (female:male).

But at this sex ratio, queens would benefit hugely by inducing their colonies to invest more (or entirely) in males.

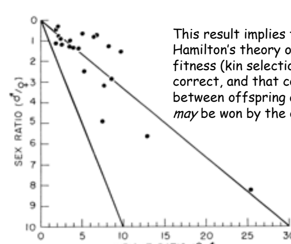
Who wins?



On average, the *workers* win!

Robert Trivers and Hope Hare estimated the average ratio of investment in female reproductives for 21 species of ants with one queen per colony.

In all cases the ratio was greater than 1:1 (the value predicted if queens are in control), and it averaged roughly 3:1 (the ratio predicted if workers are in control).



This result implies that Hamilton's theory of inclusive fitness (kin selection) is correct, and that conflicts between offspring and parents *may* be won by the offspring.

Figure 4.12. The sex ratio (males/females) as a function of the weight ratio (female/male) for 21 species of ants with one queen per colony. This famous figure illustrates the first test of the prediction that workers in some species of social Hymenoptera should tend to bias their colony's investment ratios toward female reproductives. The upper line shows the 3:1 ratio expected if the queen typically mates with just one male and the workers control the investment ratio; the lower line shows the 1:1 ratio expected if the queen mates many times or if she controls the ratio of investment. Note that in this sample of species, females are always at least twice as large as males, often five to 10 times as large, and in one case 25 times as large. (From Trivers, R. L. and Hare, H. (1976) Haplodiploidy and the evolution of the social insects. *Science*, **191**, 249–63. Copyright 1976 by the AAAS.)