Evolution of Social Behavior

Cooperative behaviors are widespread.
Why?

Group-living is widespread in the animal kingdom.
Although many species form temporary associations, such as (a) flamingo (Phoenicopterus minor) colonies and (b) zebra (Equus quagga) herds, some species such as (c) African elephants (Loxodonta africana), (d) snapping shrimps (Synalpheus brooksi), and (e) superb starlings (Lamprotornis superbus) form more permanent social groups and live together year-round.

Benefits: Protection

Wildebeest gathered into groups are more protected from predators than any solitary wildebeest.

Benefits: feeding efficiency, protection from predators

Schooling of fish

Benefits: Territory Defense, Hunting

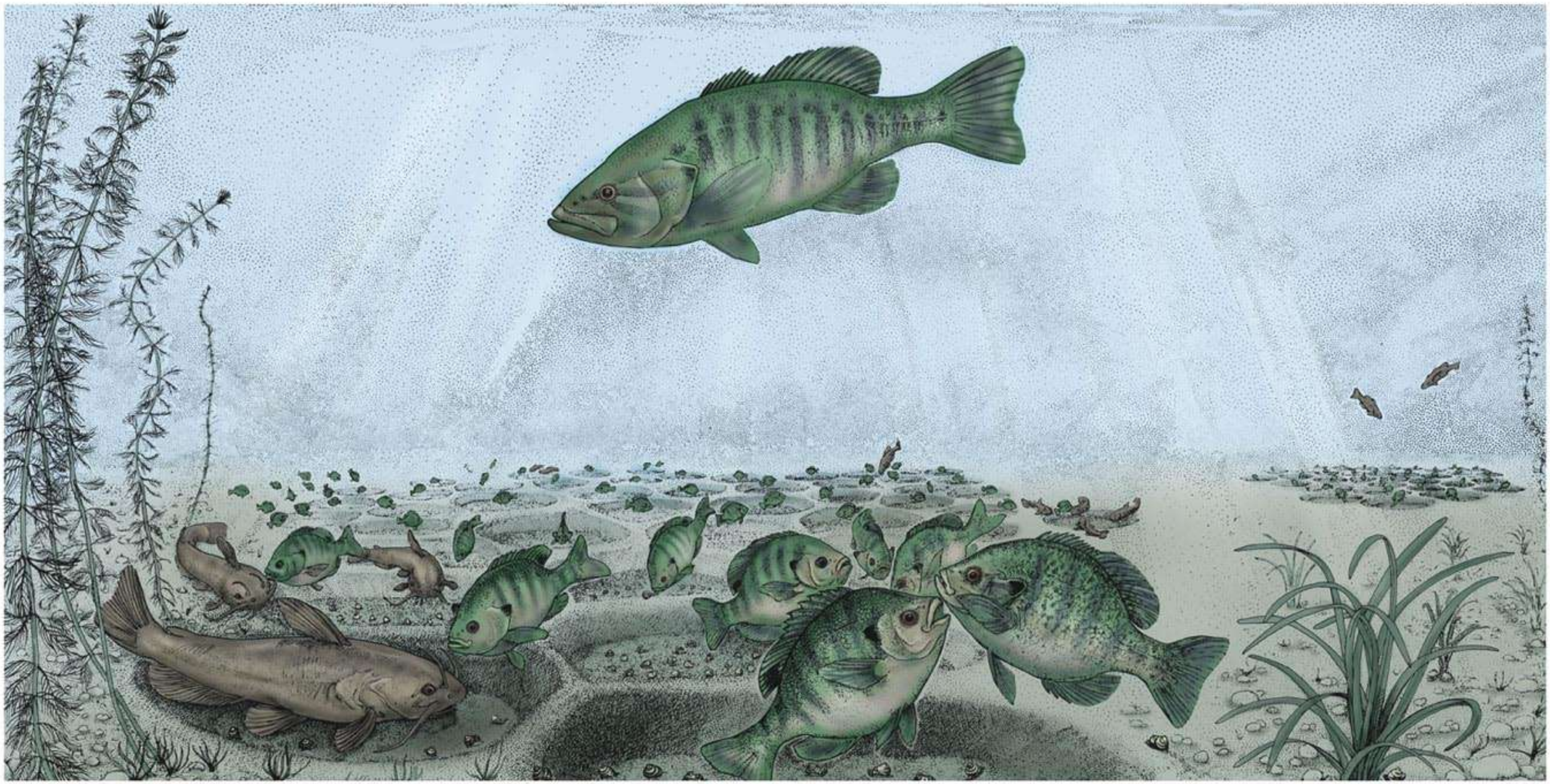
Spotted hyaena: one the most highly gregarious of all carnivores; lives in groups containing up to 90 indiv; clans defend group territories; strict dominance hierarchy.

Benefits: Cooperative Breeding

Genetically related female banded mongooses live and breed in groups, and care for each other's young

Benefits: Cooperative Breeding

Male bluegill sunfish nest colonially as defensive adaptation against egg-eating predators.



Altruism
Kin Selection

Social interaction

Social interactions between organisms present the opportunity for **conflict** and **cooperation**

Interaction between individuals can have 4 possible outcomes on the fitness of the 2 individuals involved:

Types of social interactions among members of the same species

The actor in any social interaction affects the recipient of the action as well as himself. The costs and benefits of interactions are measured in units of surviving offspring (fitness).

	Actor benefits	**Actor is harmed**
Recipient benefits	Cooperative	Altruistic
Recipient is harmed	Selfish	Spiteful

Interactions between individuals can have 4 possible outcomes in terms of fitness gains for the participants.

- **Cooperation** (**mutualism**): fitness gains for both participants.
- **Altruism**: instigator pays fitness cost, recipient benefits.
- **Selfishness**: instigator gains benefit, other individual pays cost.
- **Spite**: both individuals suffer a fitness cost.

Cooperative Interaction +/+

fitness gains for both participants

Greater Anis – communal nesting.

Nesting groups are composed of **two to four unrelated pairs** that build a single nest in which all of the females lay their eggs. All of the individuals in the group participate in territorial defense, nest-building, incubation and food delivery. Adults are apparently incapable of recognizing their own eggs or nestlings, so the young are raised in communal clutches.

Selfish Interaction +/-

instigator gains benefit, other individual pays cost

Cane Toad Tadpoles eat Cane Toad eggs

Cane toad tadpoles cannibalize eggs of their own species (but different cohort).

Helps to reduce competition in addition to giving the cannibals a nutritional boost

Spite Interaction -/-

Actor suffers loss in order to impose a penalty on recipient, both parties suffer.

No clear cut cases of spite documented

Bacterial example in textbook. Bacteria make toxin to which they are immune, but costs energy to produce, reducing growth. When toxin released it kills other competitor strains.

Altruism Interaction -/+

actor pays fitness cost, recipient benefits

In altruism, an individual reduces its own fitness to help other members of its social group.

- – inclusive fitness
- – kin selection

Meerkats: Sentries and Warning Altruistic Behevior?

Meerkats – When they leave their burrows to look for food, a few animals stand guard. The guards climb onto a rock or a termite mound and stand on their hind legs. They scan the skies for eagles and hawks. They also keep an eye out for hungry jackals. If a predator appears, the guards call quickly and sharply. This is the signal for everybody to dive into the burrows.

Altruistic Behavior – Prairie Dogs

North American prairie dogs, which are related to squirrels, also live in burrows. The burrows cover a huge area of land known as a prairie-dog town. Prairie dogs do not post guards. Yet, because there are so many prairie dogs, someone in the town is likely to spot a hawk or a coyote. Prairie dogs that spot danger will give a danger call. At this signal, everybody scurries underground to safety.

Altruistic Behavior in Humans?

Altruism is the difficult one to explain because the instigator pays a cost and another individual benefits.

Hard to see how selection could favor an allele that produces behavior benefiting another individual at the expense of the individuals bearing the allele.

If such behaviors have a genetic basis, then the elimination of altruists should cause the frequencies of altruistic genes to decrease. We would not expect alarm calls to be an evolutionarily stable strategy.

Kin selection and altruistic behavior

For Darwin, the apparent existence of altruism presented a "special difficulty, which at first appeared to me insuperable, and actually fatal to my whole theory."

However, he also suggested a solution — selection might favor traits that decreased the fitness of the actor if they increased the reproductive success of close relatives

This form of selection, which takes into account the fitness benefits to relatives is *kin selection*

Hamilton’s rule

Given r the coefficient of relatedness between the actor and the recipient, **Hamilton’s rule** states that an allele for altruistic behavior will spread if

$$Br - C > 0$$

B is benefit to recipient and

C is the cost to the actor.

Unit of measurement for B and C is surviving offspring.

Hamilton’s rule

$$Br - C > 0$$

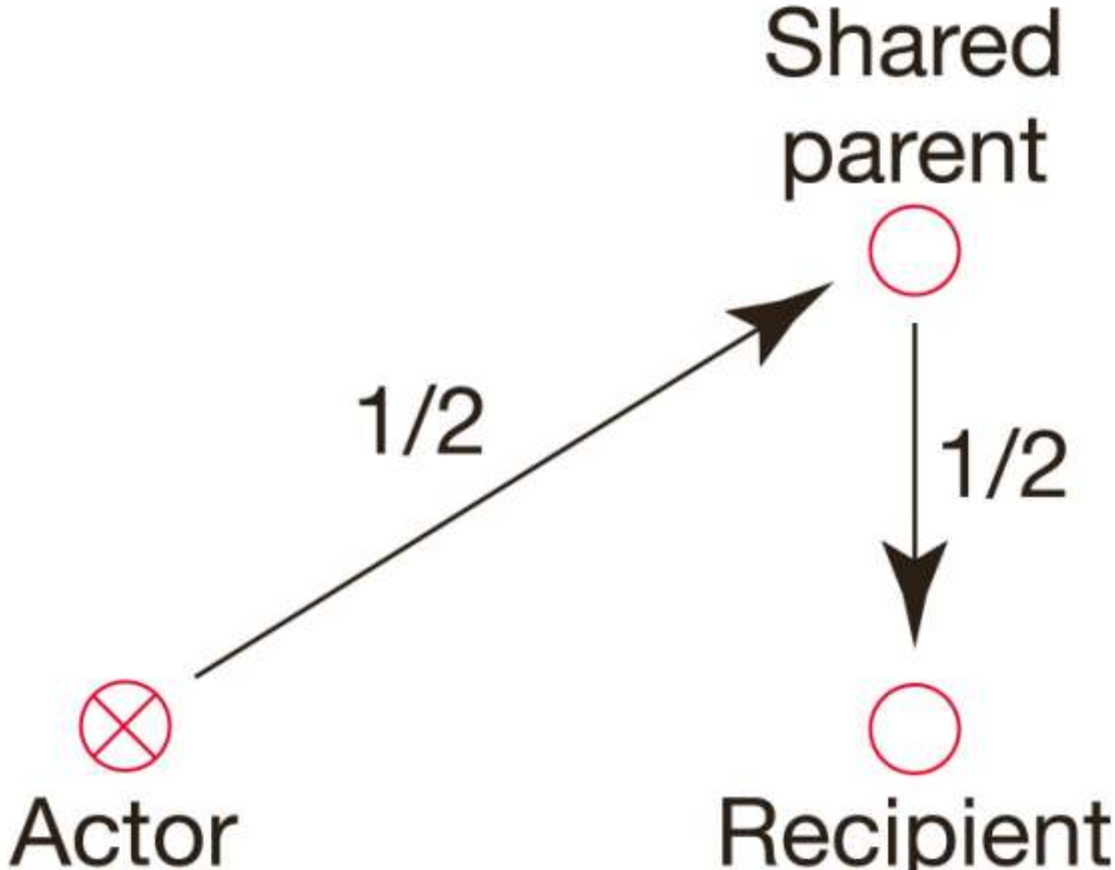
Altruistic behaviors are most likely to spread when costs are low, benefits to recipient are high, and the participants are closely related.

Calculating r

Need a pedigree to calculate r that includes both the actor and recipient and that shows all possible direct routes of connection between the two.

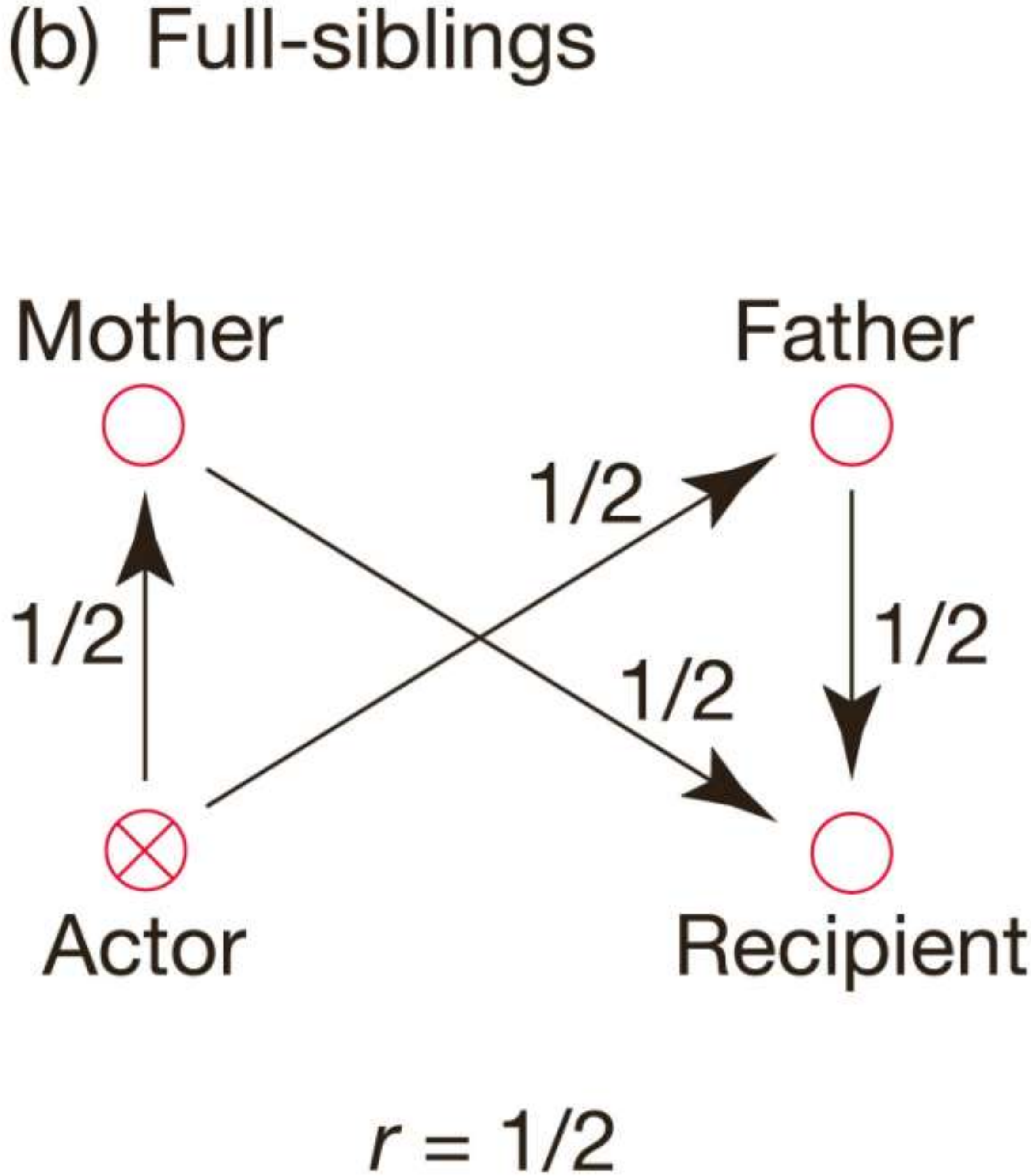
Because parents contribute half their genes to each offspring, the probability that genes are identical by descent for each step is 50% or 0.5.

(a) Half-siblings

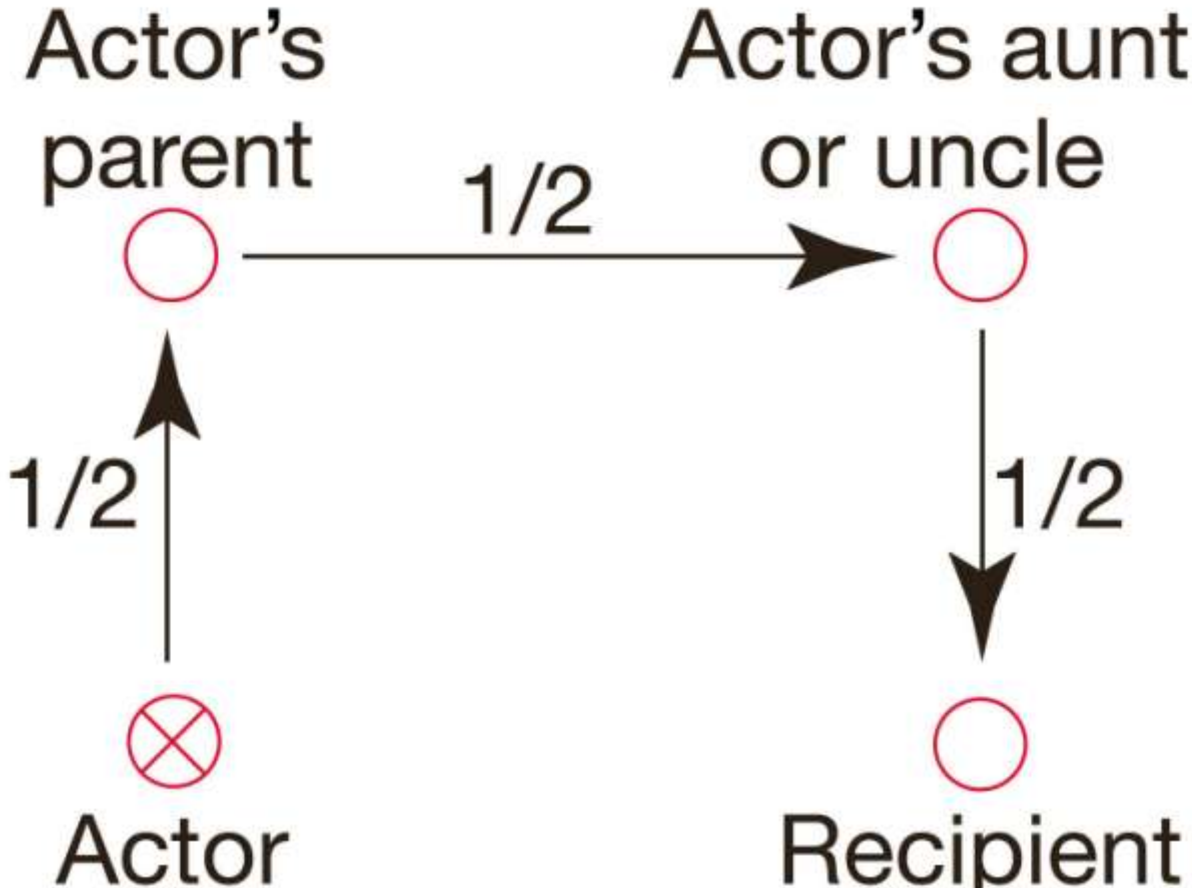


$r = 1/4$

Must add contribution from mother and father
¼ + ¼ = 1/2



(c) Cousins



$r = 1/8$

Coefficients of relationship

RELATIONSHIP	r
Mother/Child	0.50
Father/Child	0.50
Full siblings	0.50
Half siblings	0.25
Grandparent/Grandchild	0.25
Aunt or uncle/nephew or niece	0.25
First cousins	0.10

The first study to test Hamilton's rule successfully involved a wild population of red squirrels in Yukon, Canada.

Surrogate mothers would adopt related orphaned squirrel pups but not unrelated orphans.

Helping behavior in birds: White-fronted Bee-eaters

In some birds, young that are old enough to breed on their own instead help their parents rear siblings.

Steve Emlen et al. studied white-fronted bee-eaters intensively in Kenya.

Nest in colonies of 40-450 individuals. Groups of relatives (clans) defend feeding territories in vicinity of colony.

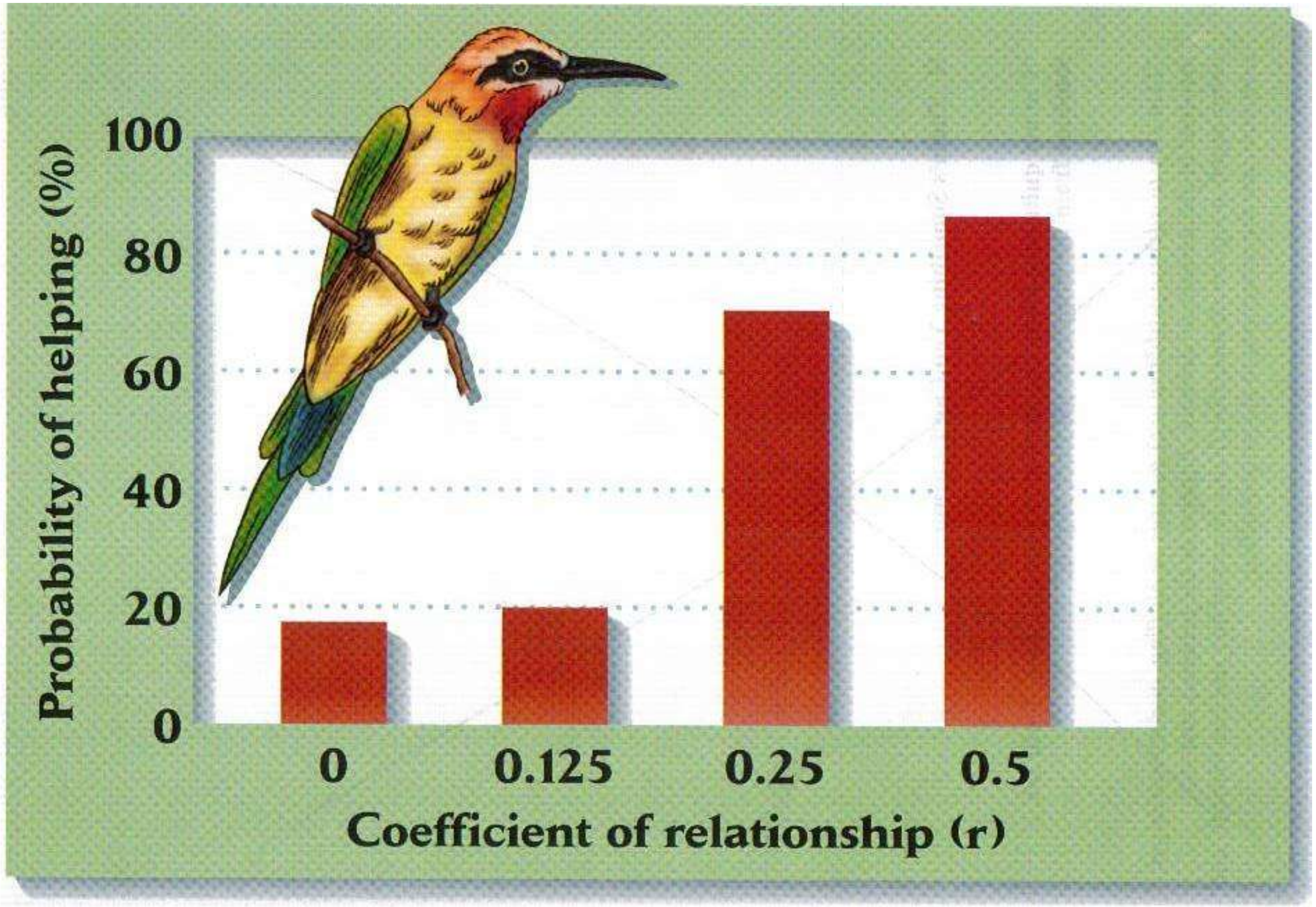
Helpers assist in nest building, nest defense and food delivery.

Helping Behavior in Birds:

White-fronted bee-eaters

Figure 12-5 Evolutionary Analysis, 4/e

Helpers at the Nest: Assist Parents



Bee-eaters conform to predictions of Hamilton’s rule.

Inclusive fitness

Hamilton invented the idea of ***inclusive fitness***. Fitness can be divided into two components:

-Direct fitness results from personal reproduction

Indirect fitness results from additional reproduction by relatives, *that is made possible by an individual's actions.*

Kin selection

Natural selection favoring the spread of alleles that increase the indirect component of fitness is called **kin selection**.

Mechanisms of Kin Recognition?

One mechanism for direct kin recognition uses MHC proteins

Major Histocompatibility Complex (MHC) glycoproteins are important to immune response

- MHC receptors bind to bits of virus inside an infected cell

- move to surface, flag down killer T cells to nuke the cell

Are responsible for tissue rejection after organ transplant

- there are so many alleles, only close relatives are likely to share alleles

- these genes are probably good markers for kinship

Mechanisms of Kin Recognition

Experiment: Do mice that nest communally use MHC recognition to distinguish relatives from non-relatives?

- MHC proteins are released in mouse urine (signal is there)

- mice can tell full from half-siblings by their MHC genotype

- mothers tend to place their young in nests that contain other young sharing their MHC alleles

Thus, mice use MHC proteins to identify allelic similarities among offspring they may end up nursing

why? maternal investment is thus directed to offspring and close relatives

Cooperation among non-relatives: Vampire Bats

Vampire bats will starve to death if they go 3 nights w/out feeding

Bats that roost together
meals
to their roost-mates

Do bats regurgitate to

(1) relatives?

(2) bats who they are just around a lot?

Cooperation among non-relatives: Vampire Bats

<u>Hypothesis</u>: Bats reciprocate blood sharing with frequent roostmates

<u>Experiment</u>: 9 bats held in captivity for several weeks

- each night, food was withheld from a different bat
- so who fed whom?...

<u>Result</u>: Bats fed other bats who had previously fed *them*

- in other words, cooperation based on reciprocity: I help you now, you help me later

Reciprocal altruism

Reciprocal altruism most likely in social animals where individuals interact repeatedly because they are long-lived and form groups, and also when individuals have good memories.

Eusociality

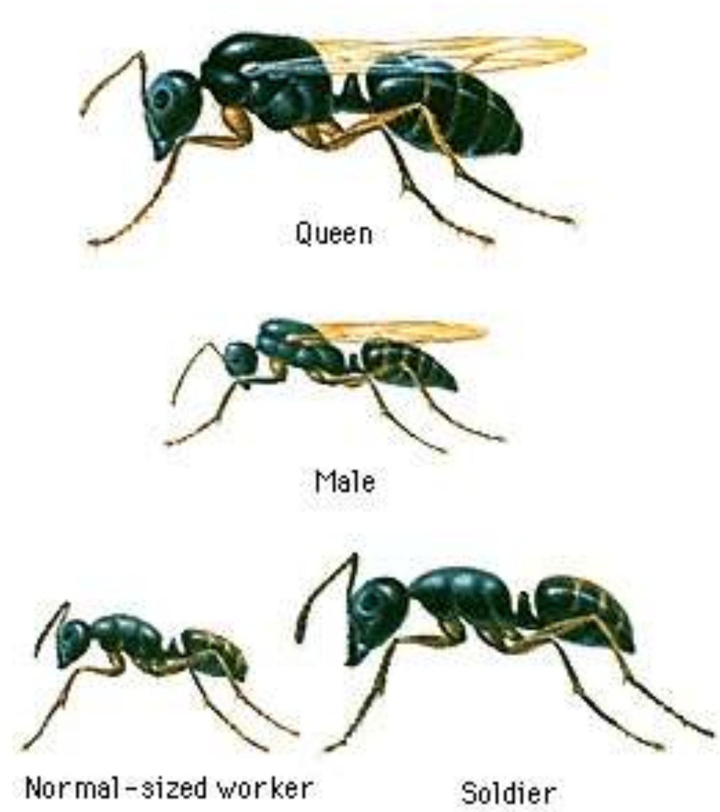
Evolution of Eusociality

Eusociality (true sociality).

Many eusocial insects (bees, ants, termites) have **castes** that do not reproduce. Instead they act as helpers at parents nests for their entire life. This is an extreme type of altruism.

Darwin found social insects to be "one special difficulty, which at first appeared to me insuperable, and actually fatal to my whole theory".

How could the worker castes of insect societies have evolved if they were sterile and left no offspring?



Honeybees – Cooperative Brood care

Apparent altruism occurs on 2 levels in honey bees:

(1) Self-sacrifice in eviscerating themselves when they sting something that is threatening their colony; and

(2) (2) that the workers in the hive do not reproduce, but help the queen reproduce instead.

Major and minor workers of leafcutter ants

Termite Queen and Workers

Naked Mole Rats
East Africa

Live in large colonies underground.

Only one female (the queen) and one to three males reproduce, while the rest of the members of the colony function as workers.

Eusociality: the ultimate in reproductive altruism

Characteristics of eusociality

- Overlap in generations between parents and offspring
- Cooperative brood care
- *Specialized castes of non-reproductive individuals*

Insects (termites, hymenoptera), snapping shrimp, naked mole rats

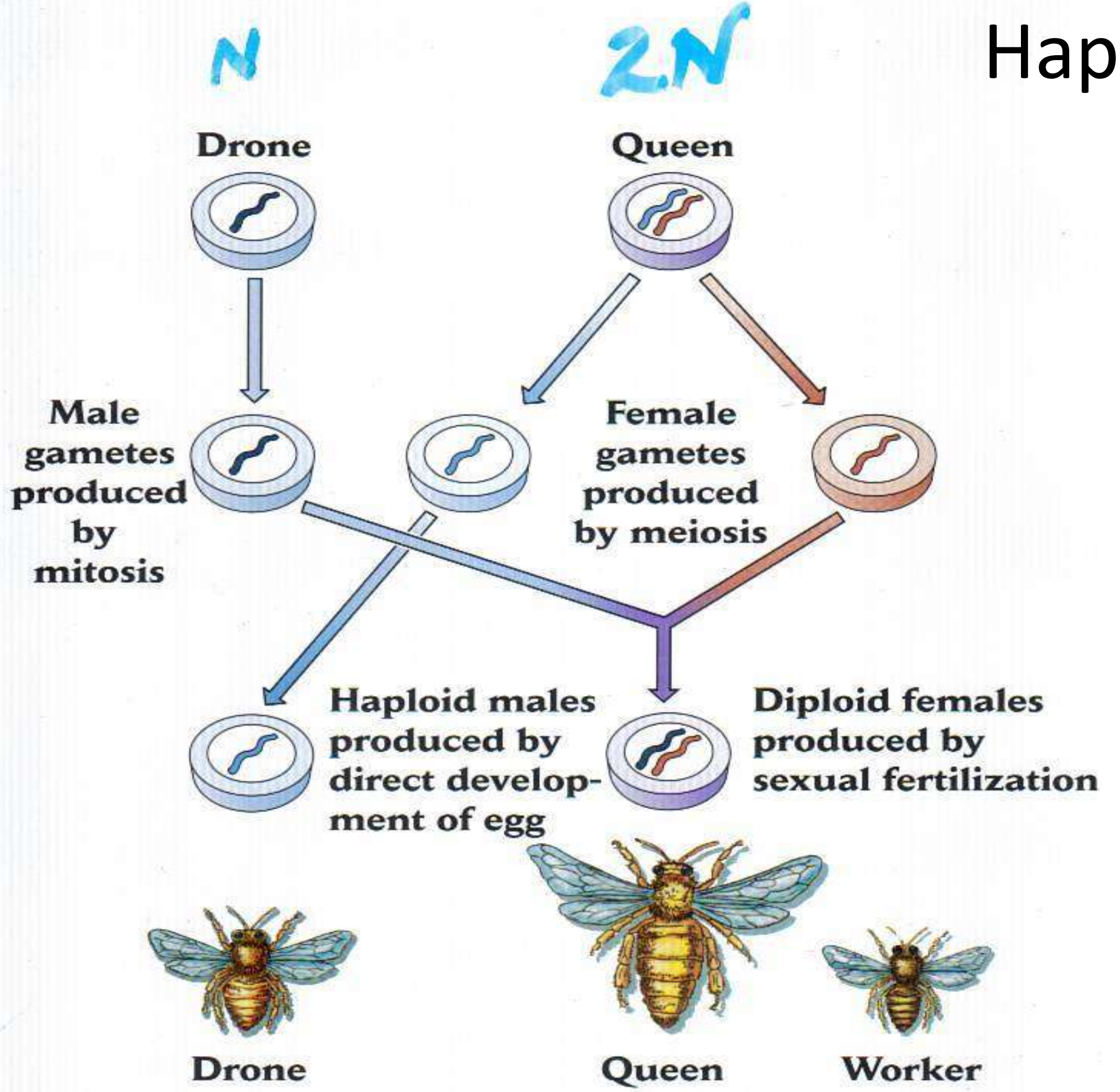
Haplodiploidy and Eusocial Hymenoptera

One idea advanced to explain eusociality is the unusual genetic system (Haplodiploidy) of the Hymenoptera (ants, wasps, bees).

Males are haploid and females diploid.

Males develop from unfertilized eggs and females from fertilized eggs.

Haplo-Diploidy



Ricklefs, THE ECONOMY OF NATURE, Fifth Edition

Figure 12-18

T-154

Haplodiploidy and Eusocial Hymenoptera

Daughters receive all of their fathers genes and half of their mothers genes. Thus, **daughters share ¾ of their genes**.

According to the theory of kin selection, a sister is more valuable than a daughter. Females may maximize inclusive fitness by being sterile workers and helping to produce reproductive sisters (rather than by being reproductives themselves)

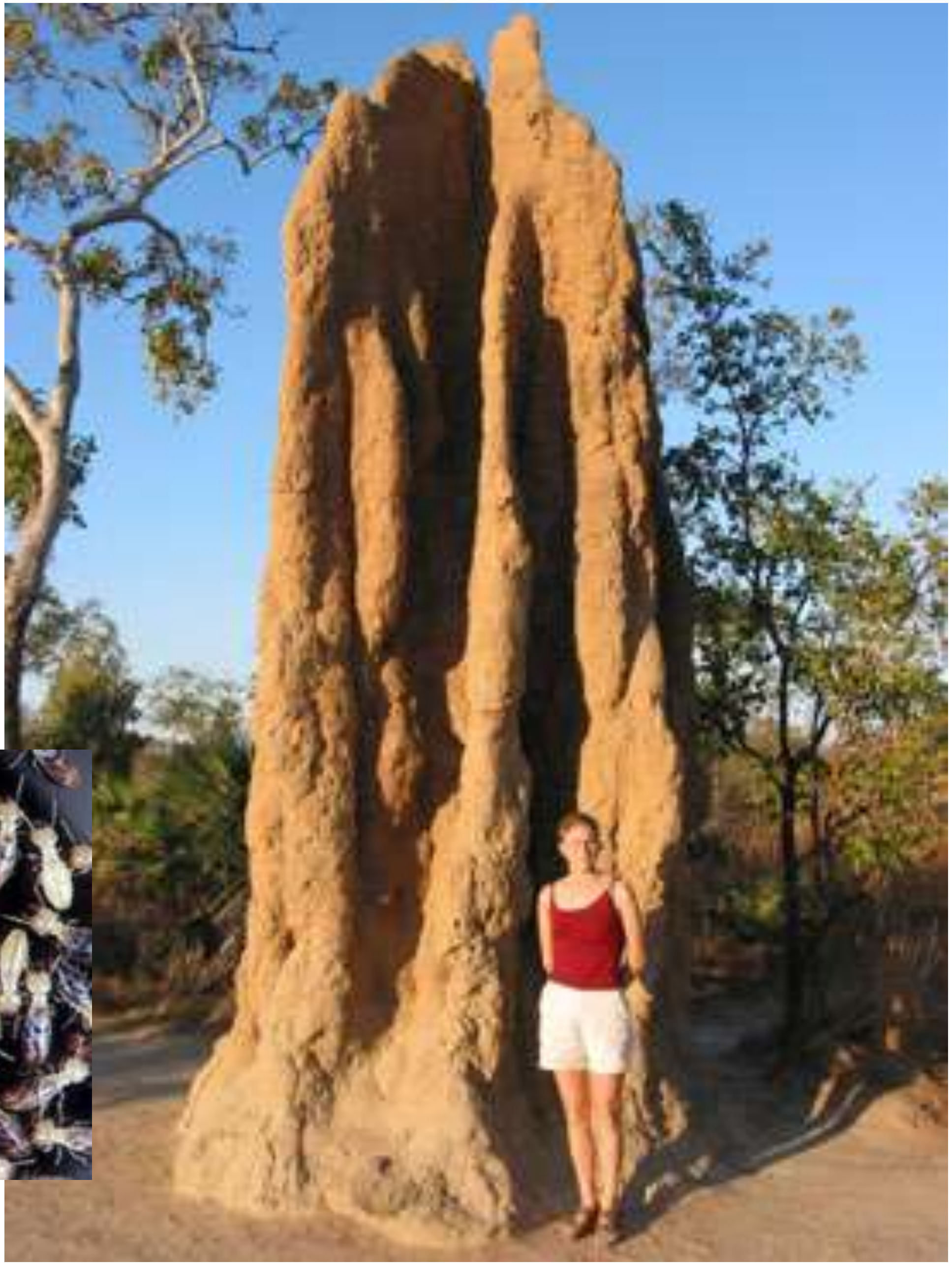
Is haplodiploidy the explanation of eusociality in hymenoptera?

Probably not

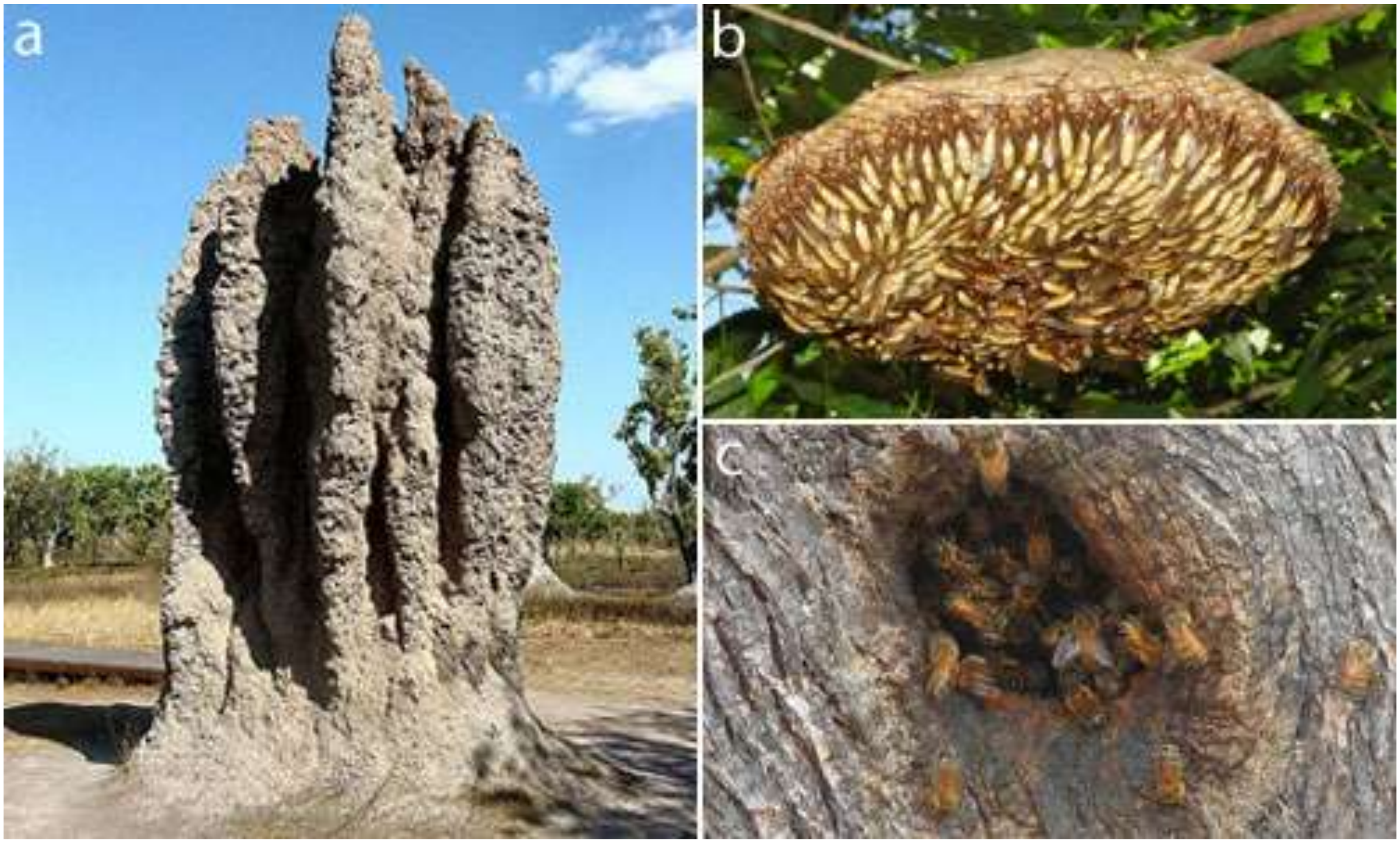
- Assumed only 1 male fertilizes a queen — this is not true in honeybees, for example
- In some species, colonies may be founded by more than 1 queen
- Some eusocial non-hymenoptera are diploid (e.g., termites)
- Many hymenoptera are not eusocial

Eusociality may have three independent origins associated with nest-building and the need to supply larvae with food)

Haplodiploidy may facilitate the evolution of eusociality but a more important factor may be the need for help in rearing young.




Social insects have well protected or defended nests, including termites (a), wasps (b), and bees (c).



Naked Mole-rats

Naked mole-rats are highly unusual mammals.

They are nearly hairless and ectothermic. They are eusocial and, like termites, can digest cellulose with the help of bacteria in their gut.

Naked Mole-rats

Colony may include as many as 200 individuals but there is only a single reproductive female (queen) and 1-3 reproductive males.

Remaining individuals act as workers. They dig tunnels to find food, defend the tunnel system from other mole-rats, and tend the young.

Naked Mole Rats

Naked mole rats

All young in a colony produced by a single queen and 2 – 3 reproductive males

Not haplodiploid, but colony members are highly inbred (average $r = 0.81$)

85% of matings are between full-sibs or parents and offspring

Queens use physical dominance to coerce help from less closely related individuals

Naked mole-rats have highly inbred colonies

Naked Mole-rats

- Leading hypothesis for why naked mole-rats are eusocial is inbreeding.
- Average coefficient of relatedness is 0.81 and about 85% of matings are between parents and offspring or between full siblings.
- Despite high level of relatedness conflicts still occur because reproductive interests of workers and reproductives are not identical.

End