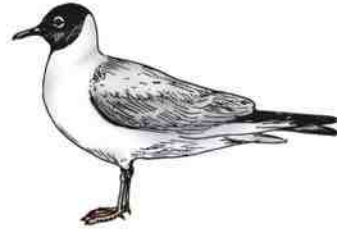


Mobbing behavior of colonial, ground-nesting gulls

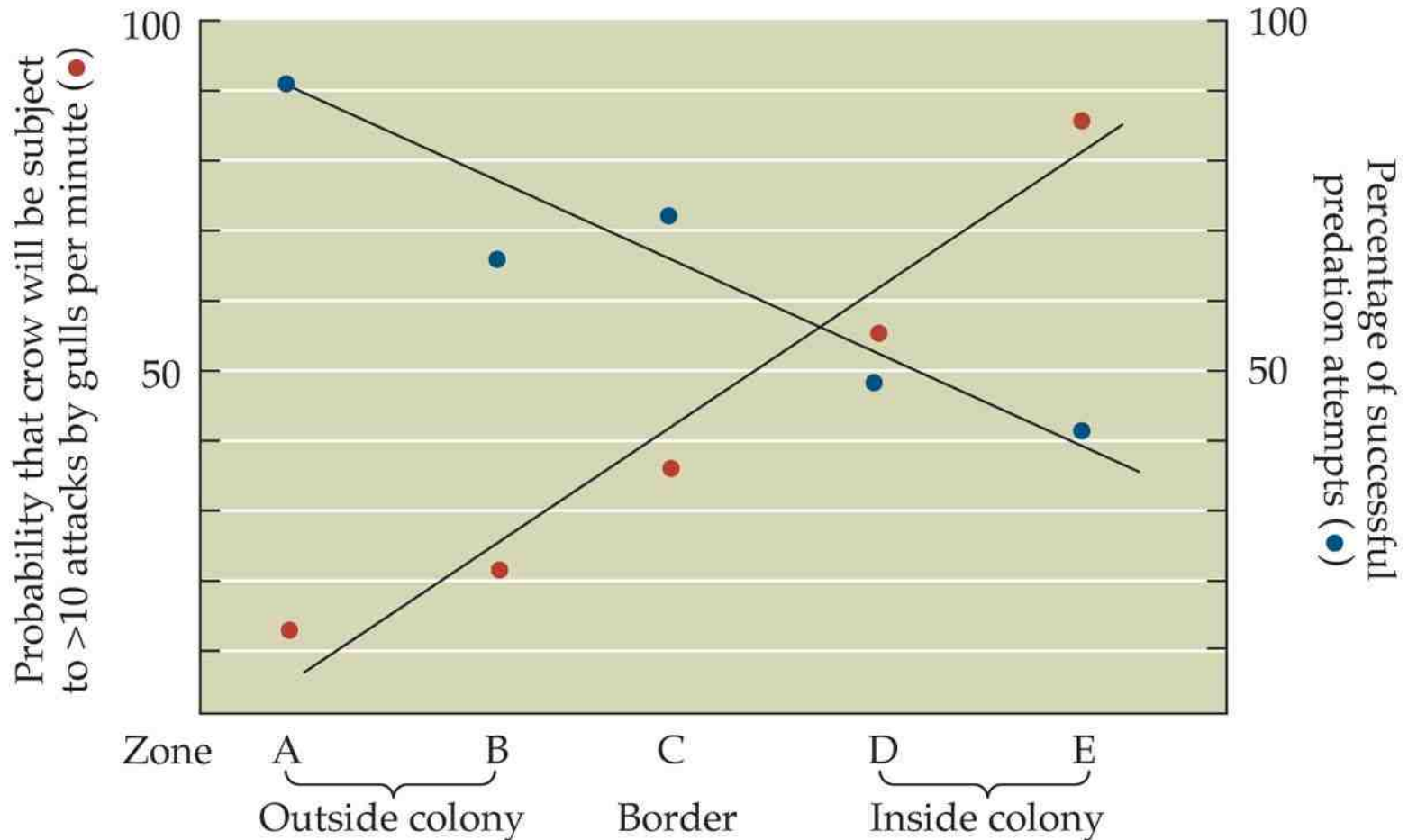




Does mobbing protect eggs?



Black-headed gull



Evolution of social behaviour

Types of groups

- Aggregation: because of environment
 - Temperature, hiding place
 - Clustered source (e.g. water hole)
- Social groups
 - Anonymous
 - Open (e.g. flock of starlings)
 - Closed (e.g. honey bee colony)
 - Individualised (e.g. chimps, wolves)

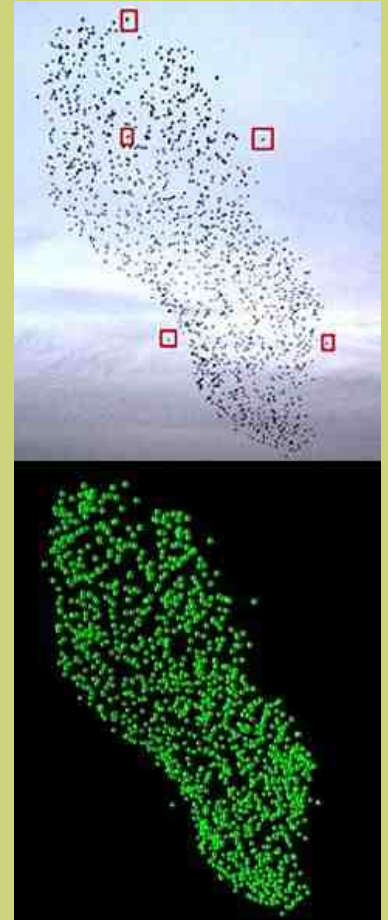
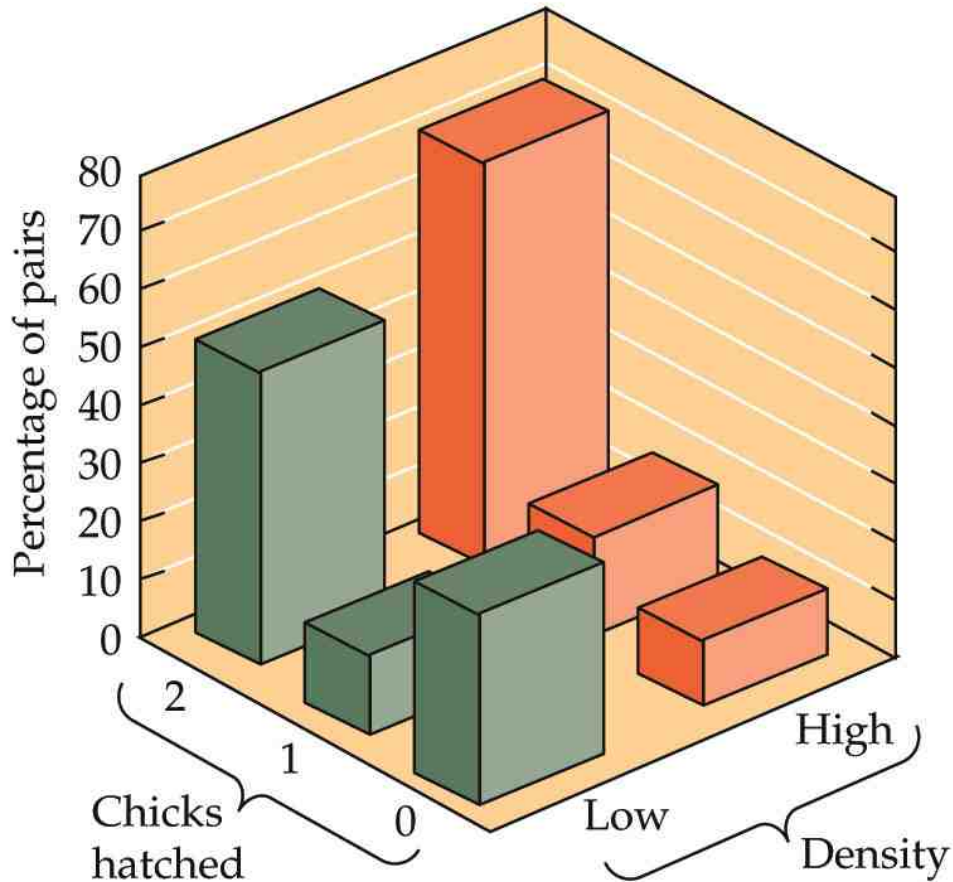


TABLE 13.1 *Some potential costs and benefits of social living*

Costs	Benefits
Greater conspicuousness of clumped individuals to predators	Defense against predators via the dilution effect or via mutual defense (see Chapter 6)
Greater transmission of disease and parasites among group members	Opportunities to receive assistance from others in dealing with pathogens
More competition for food among group members	Improved foraging via the information center effect (see Chapter 7)
Time and energy expended by subordinates in dealing with more dominant companions	Subordinates are granted permission to remain safely within the group
Greater male vulnerability to cuckoldry	Opportunity for some males to cuckold others
Greater female vulnerability to egg tossing, egg dumping, and other forms of reproductive interference by others	Opportunity to toss the eggs of others, to dump eggs in others' nests, and to interfere with rivals' reproduction

Benefit of high nest density for the arctic skua



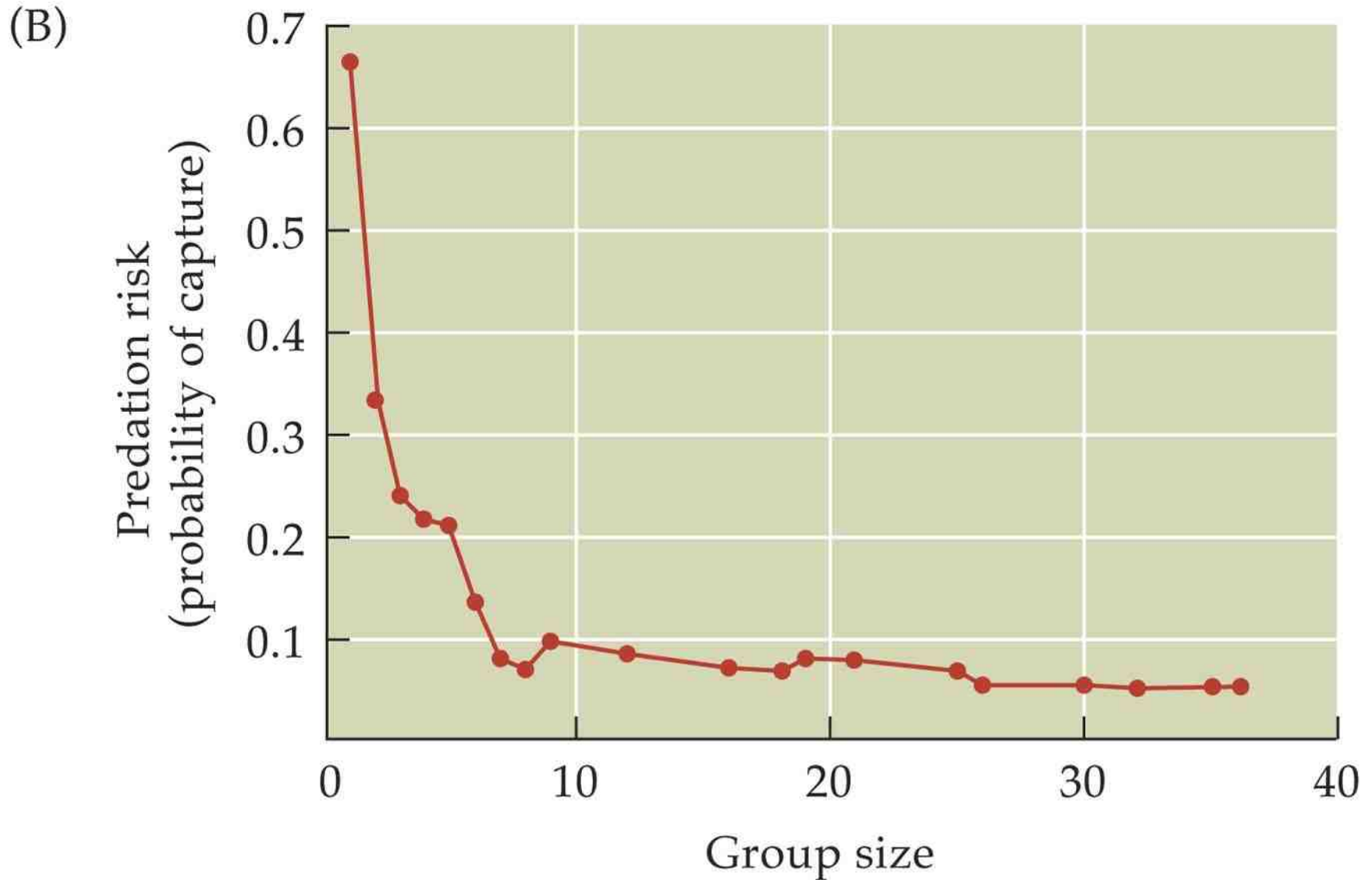
Arctic skua

The dilution effect in butterfly groups (Part 1)

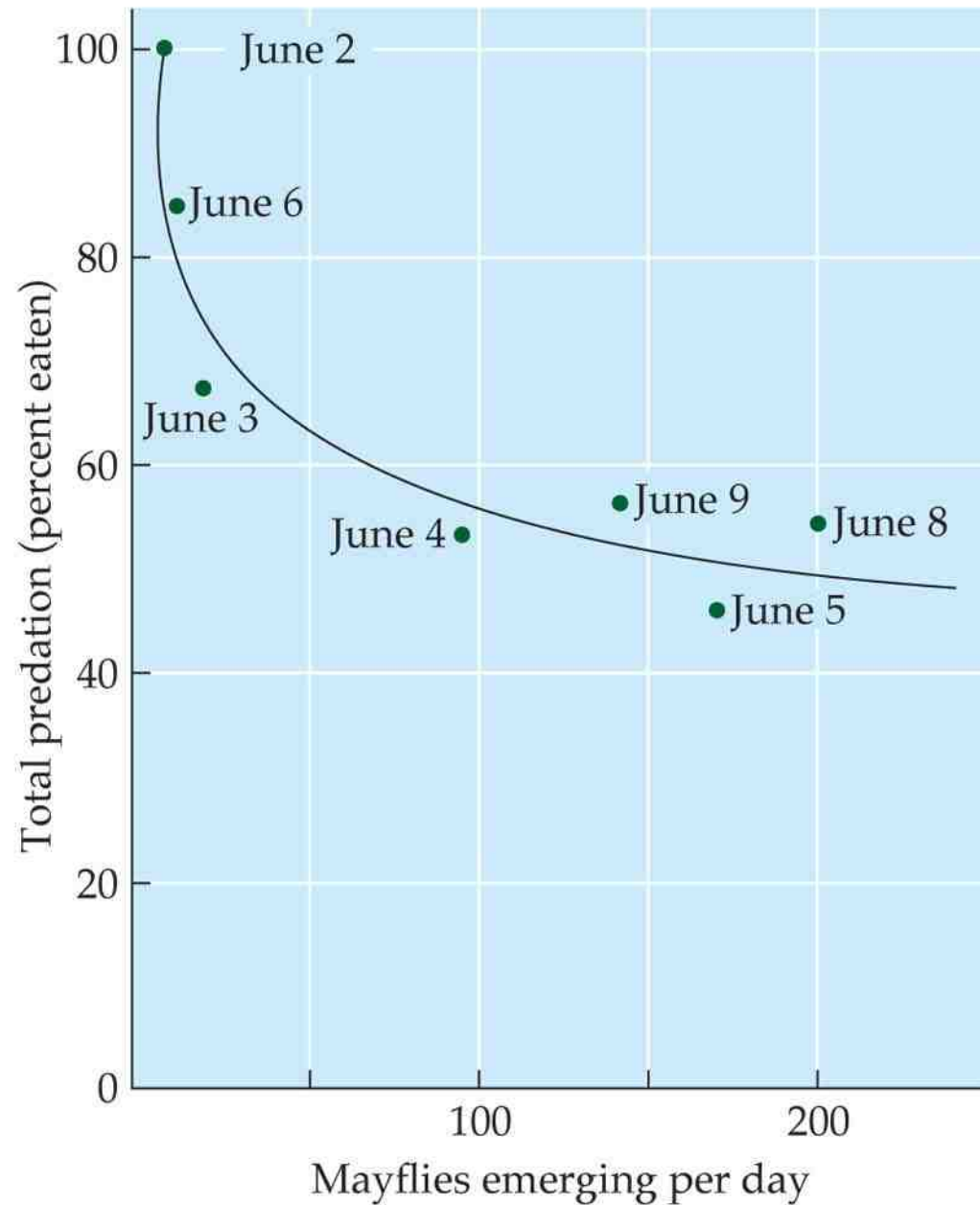
(A)



The dilution effect in butterfly groups (Part 2)



6.11 The dilution effect in mayflies



“Selfish herd” - Hamilton



Parasites



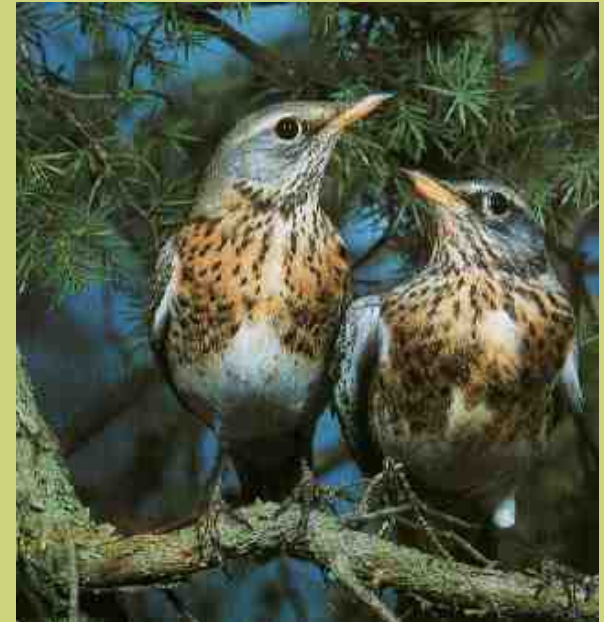
Clift swallow nestlings from normal nest and from nest fumigated with insecticide (345 nests in colony)

Parasites

Higher infection rate!
Cooperation in defense?



Competition for food



Fieldfare (*Turdus pilaris*)

- Nesting colonies
- Large colonies → diminished survival of chicks

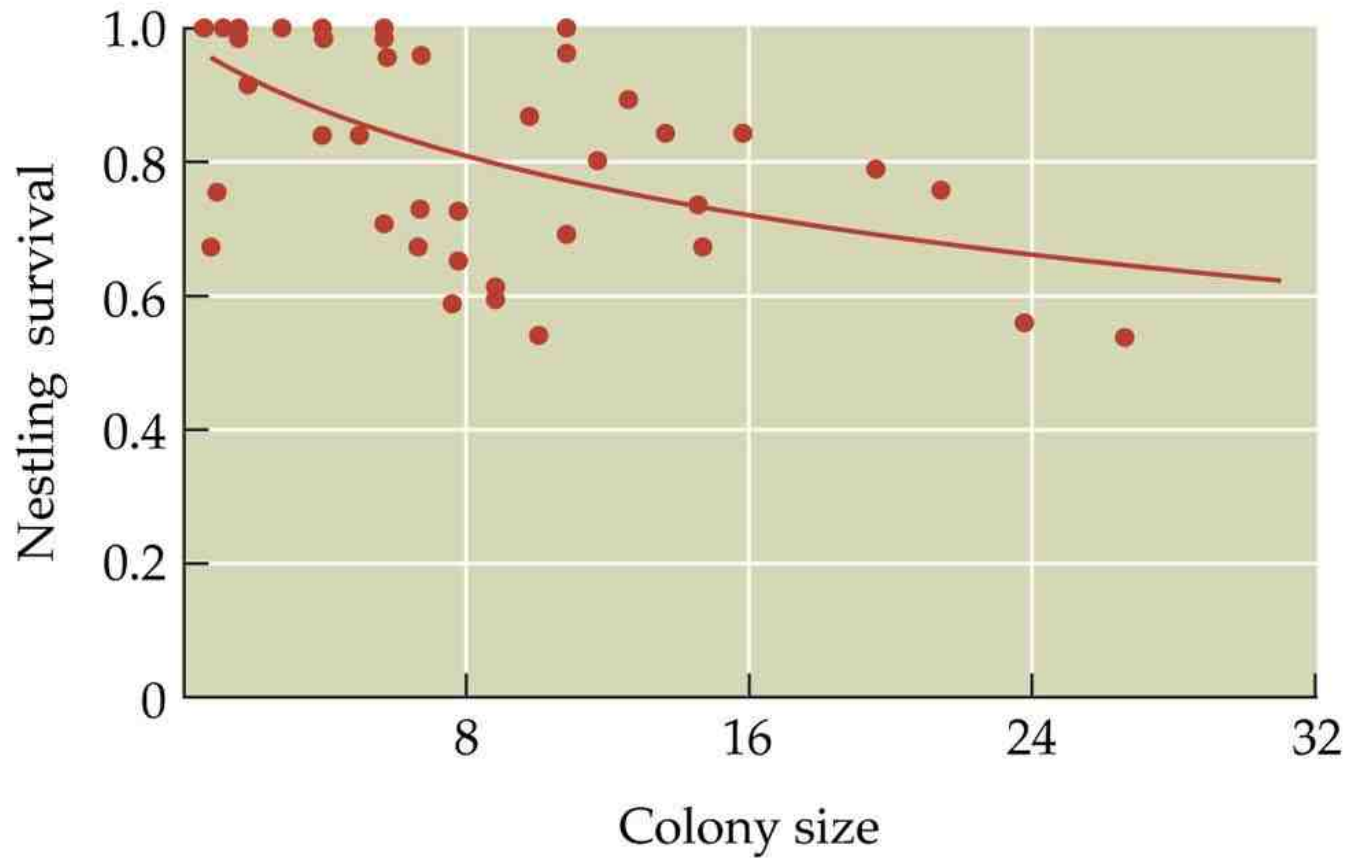


© - josedl hlašek
www.hlascek.com
Turdus pilaris 8648

performed by G. Gammochi
www.behav.org



Fieldfare



Improved foraging: information centre

Osprey (*Pandion haliaetus*)

- nesting in colonies
- searching fish shoals



Information centre



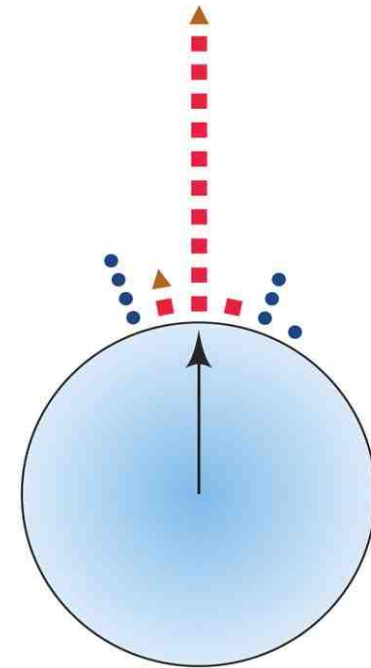
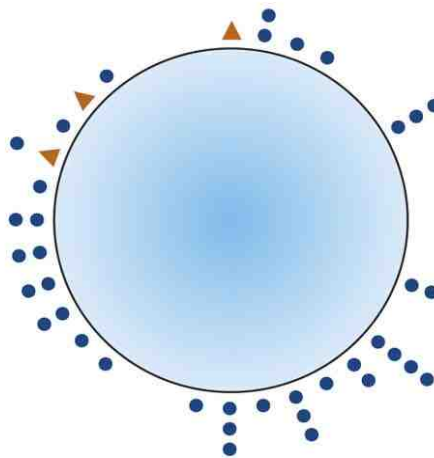
© www.LaptevProductions.com

(A)

No osprey returns
with prey

An osprey returns
with alewife

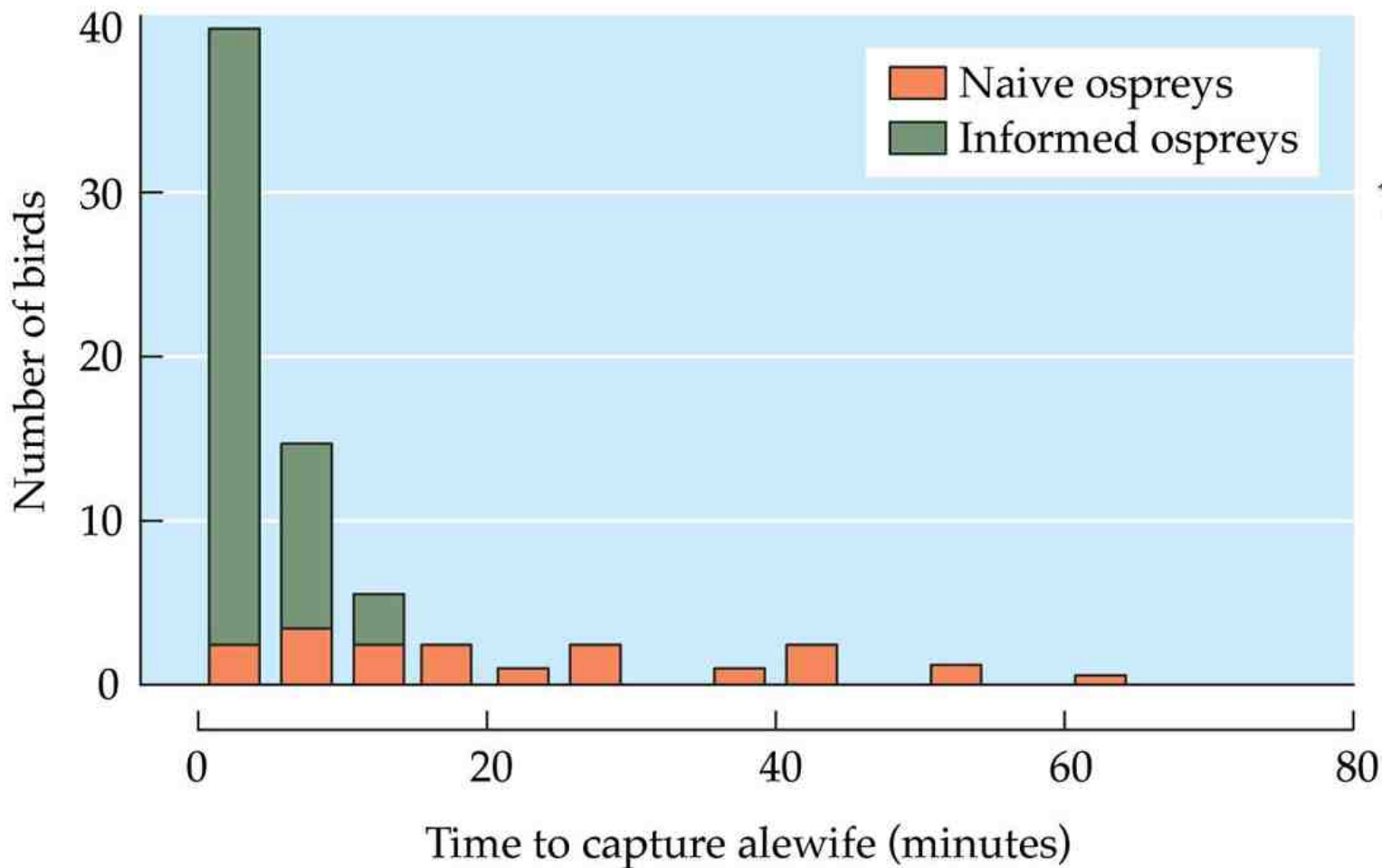
■ 10 Departures
▲ 5 Departures
● 1 Departure



Orientation of departing ospreys

Information centre

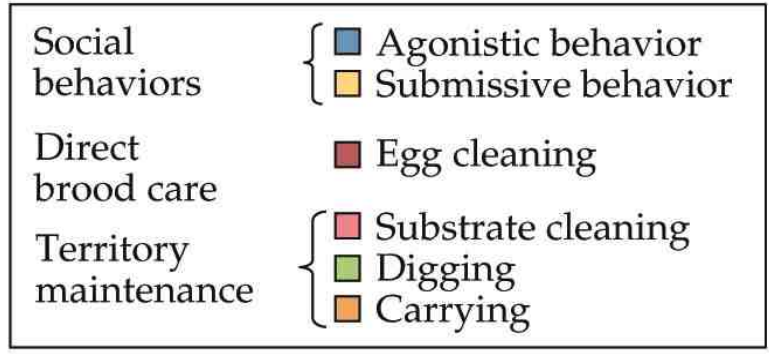
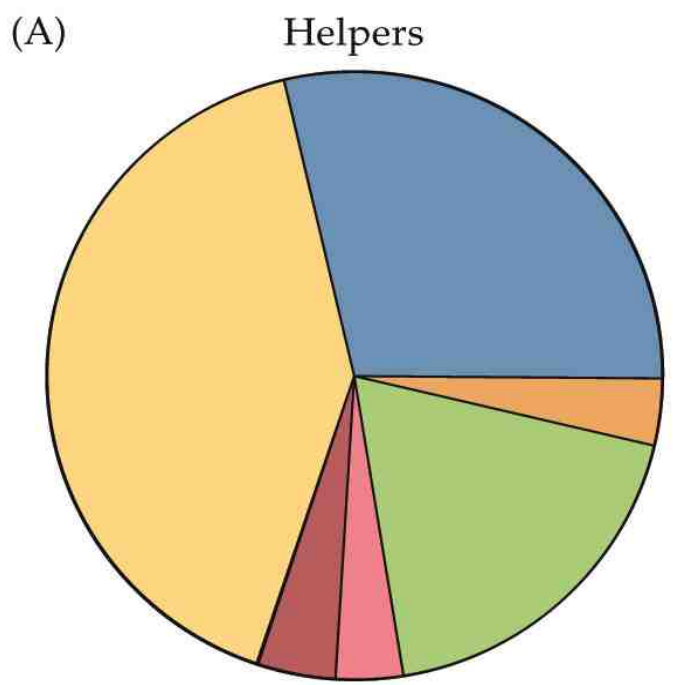
B) informed osprey finds food earlier



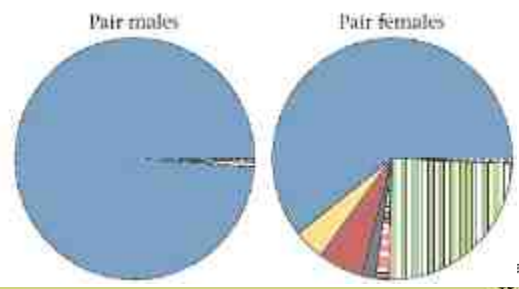
Cooperative hunting



Energy budget of subordinate, nonbreeding “helpers” that associate with breeding pairs in the cichlid fish *Neolamprologus pulcher*

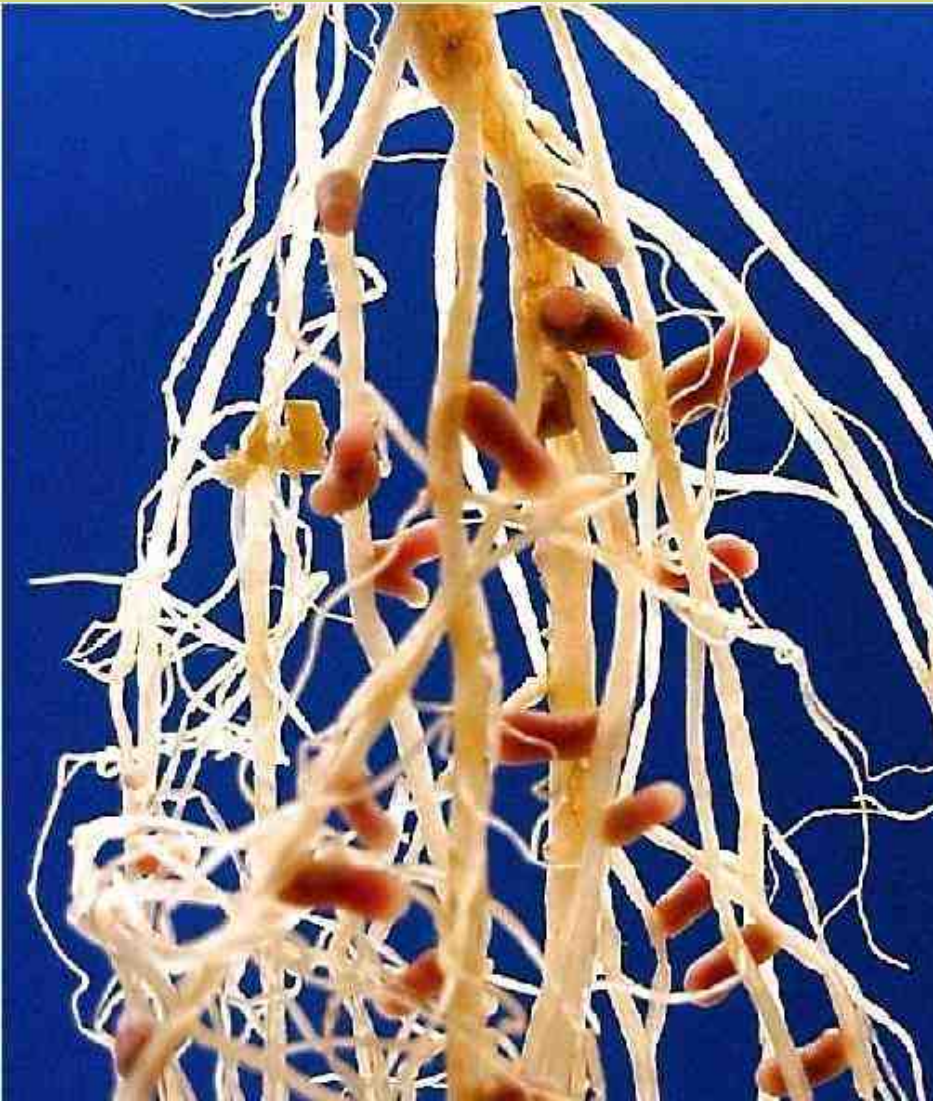


Helpers at the nest can raise fitness of hosts by defending territory, cleaning etc.
 Signaling submission is costly



ANIMAL BEHAVIOR 9e, Figure 13.1

Mutualism (interspecific): Leguminose-*Rhizobium* mutualism



Rhizobia bacteria fix nitrogen from the atmosphere which the plant can use as nutrition. The plant harbours these bacteria in specially adapted organs (nodules).

Both the plant and the bacteria benefit.

But would bacteria that do not fix nitrogen not have an advantage?

Kiers et al. 2003: No, *Rhizobia* bacteria that do not fix nitrogen are sanctioned (killed) by the plant

Reciprocity

Helping non-kin pays if it is payed back

Vampire bats

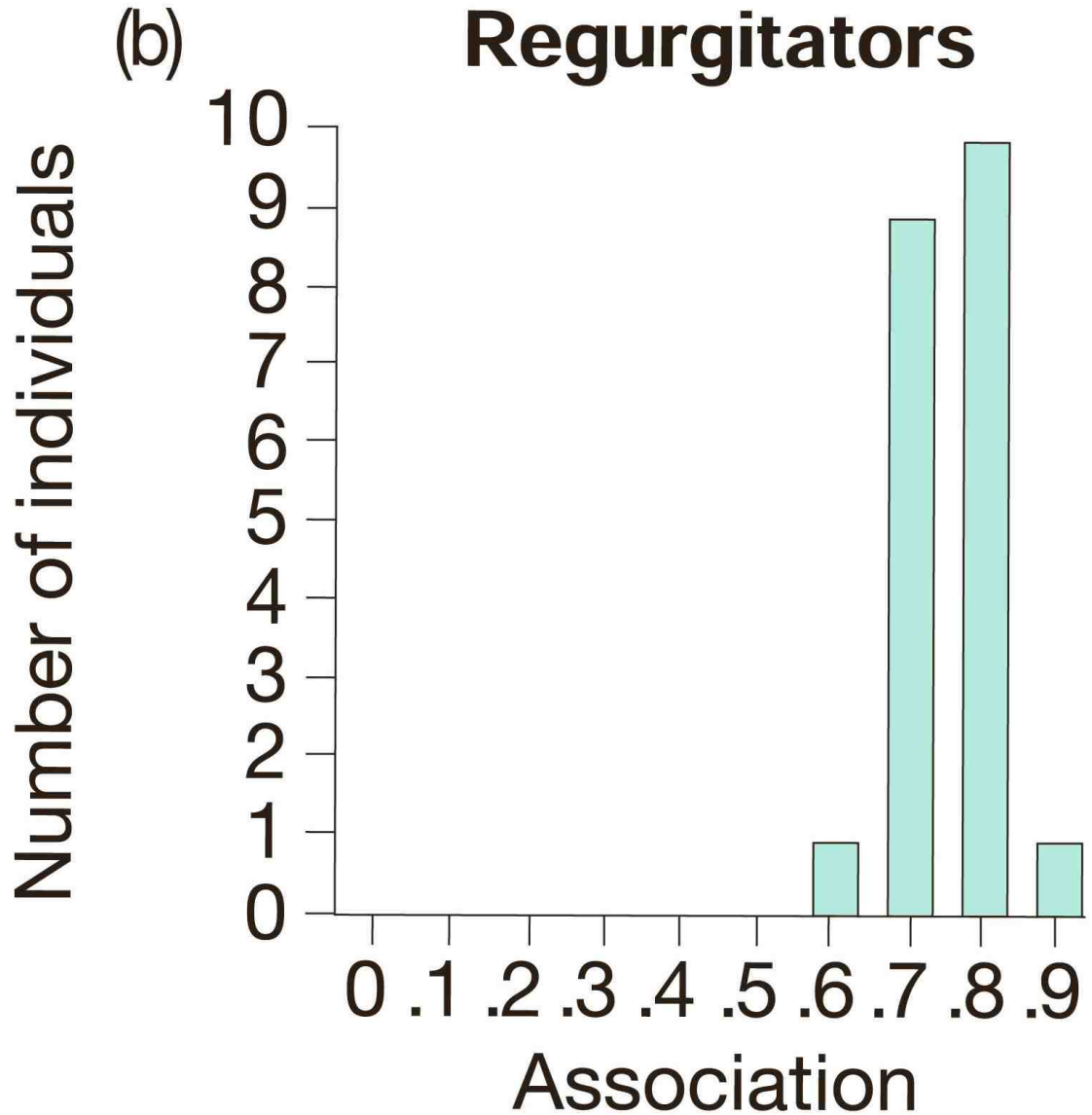
Difficult to find host

If lucky, they suck lots of blood

If not, survive only 4 days

Bloodsharing: well fed individuals regurgitate blood and donate it to others

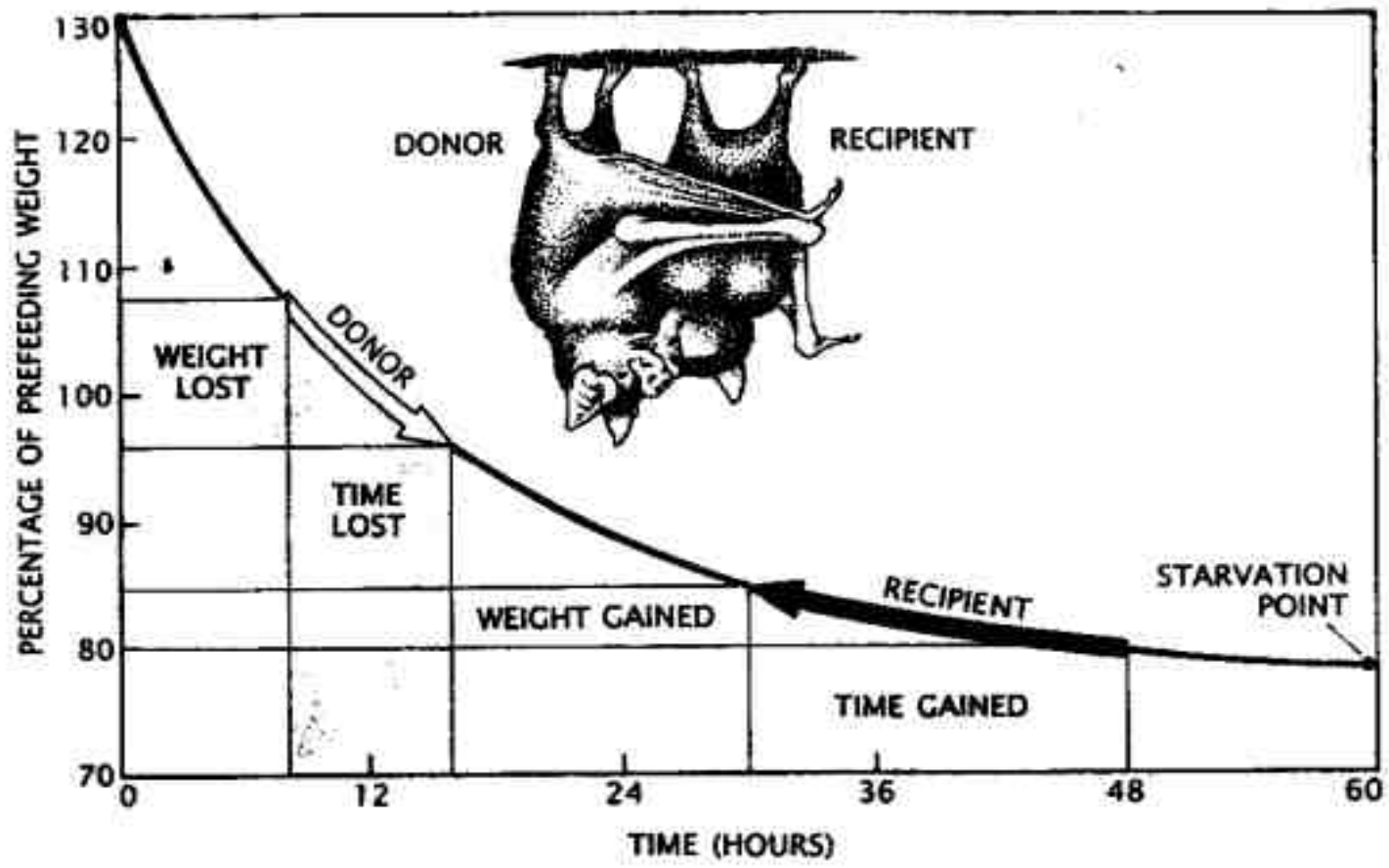




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They give blood
to individuals
they hang out
with
Kin and non-kin

Donor loses 6 hours, recipient gains 18 hours



COST-BENEFIT ANALYSIS of blood sharing among vampire bats indicates that recipients benefit more than donors lose. The author weighed adult females returning to the roost after feeding and then weighed them every hour for the next 24 hours. An individual who had fed might return at 130 percent of its prefeeding weight (half the weight of a blood meal is lost through urination within the first hour after feeding), whereas a bat who failed to feed on two successive nights might return at 80 percent of its earlier weight. By regurgitating five milliliters of condensed blood to a hungry roostmate, the donor bat might drop from 110 to 95 percent of its prefeeding weight but lose only six hours of the time it has remaining until starvation. The

Evolution of social behaviour

Helpers at the nest

White-fronted Bee-eaters
(*Merops bullockoides*)

Steve Emlen's study in Kenya



Evolution of social behaviour

Colonial nesting: 40-450 individuals

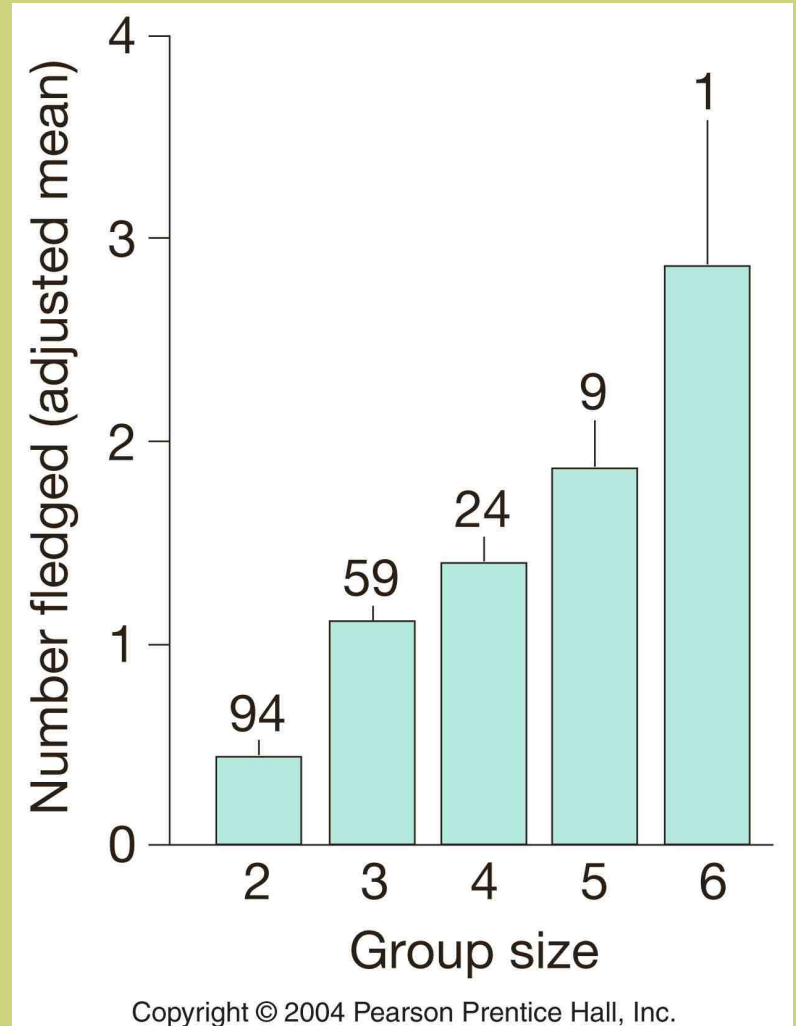
Relatives in clan defend territory

One year old birds do not reproduce, but
either join older pairs or wander about

Helpers aid close relatives

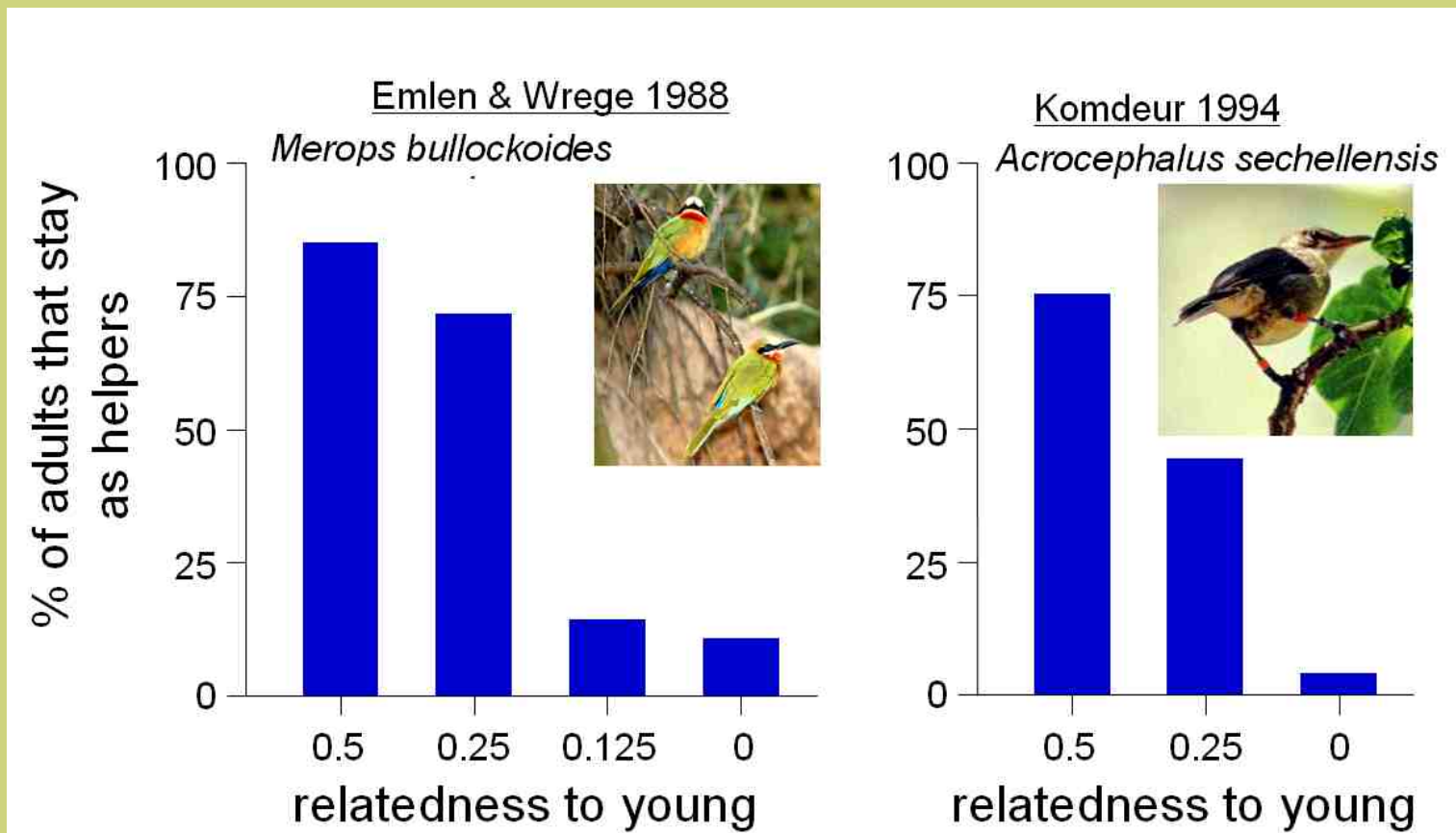
Evolution of social behaviour

Assistance of helpers is of enormous benefit to parents. More than 50% of bee-eater young starve before leaving the nest.

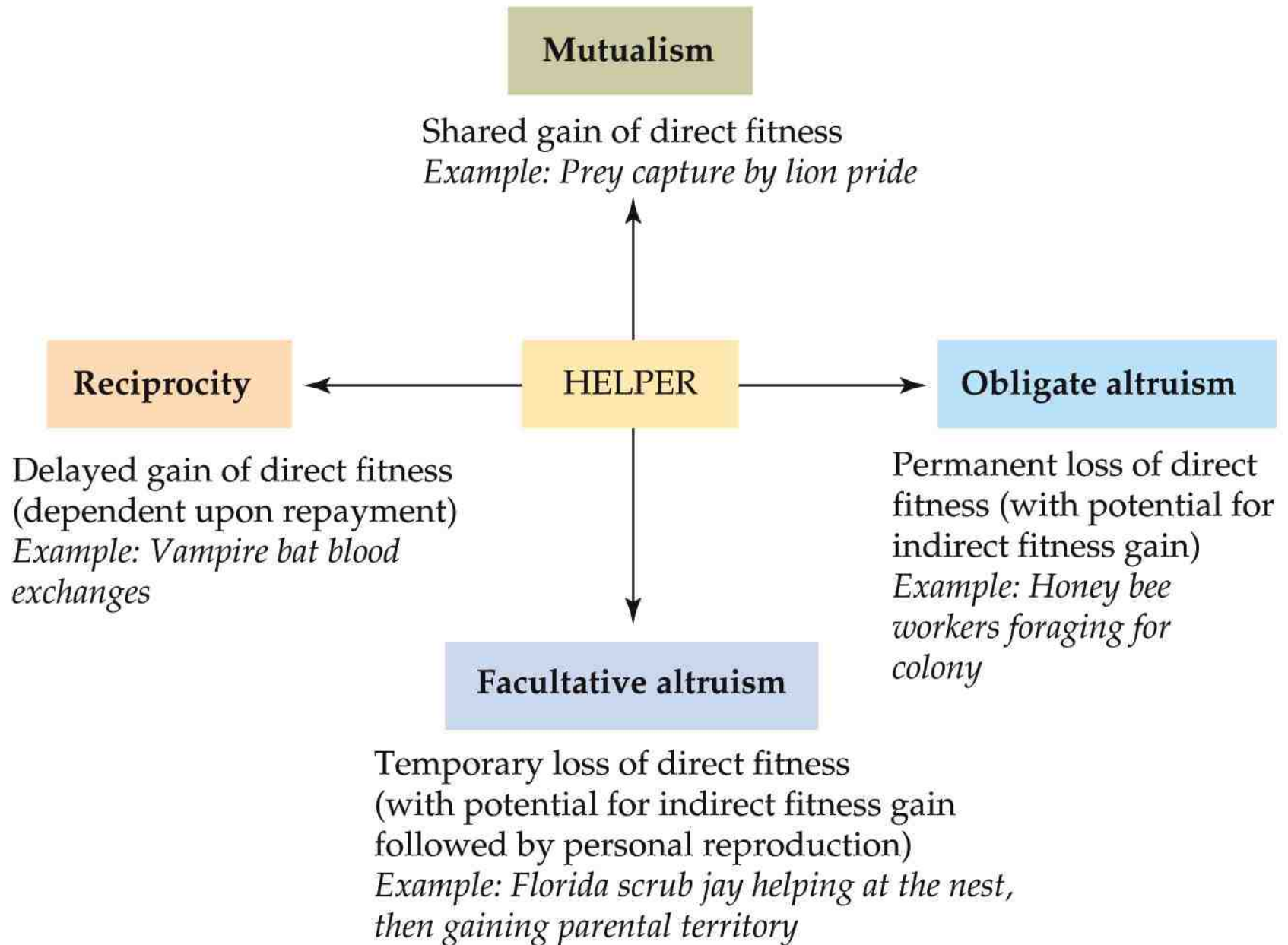


Evolution of social behaviour

Most helpers are kin



The different categories of helping behavior



Altruism

Altruist action: costly for donor, beneficial for receiver.

Word comes from French word *autrui* (others).

How can it spread?

Traditional view: group selection.

„he who was ready to sacrifice his life, as many a savage has been, rather than betray his comrades, would often leave no offspring to inherit his noble nature... a tribe including many members who...were always ready to give aid to each other and sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection” Darwin

Group selection (Wynne-Edwards)

Selection at the level of groups

Can work only in small, isolated groups.

If there is gene flow among groups a selfish mutant can spread rapidly.

Kin selection

Genetically related individuals carry the same genes with higher probability than non-kins

e.g. parent – offspring, siblings: 50% of genes are the same

Grandparent – grandchild, uncle – niece: 25% of genes are identical

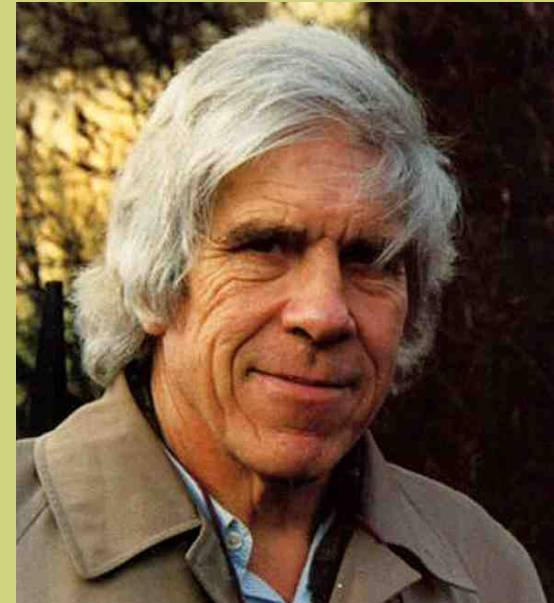
Degree of genetic relatedness (R): probability of having identical genes.

he who was ready to sacrifice his life leaves no offspring, however, his „altruistic” genes can be passed by his relatives

Kin selection

Hamilton's rule (inclusive fitness)

$$B * r > C$$



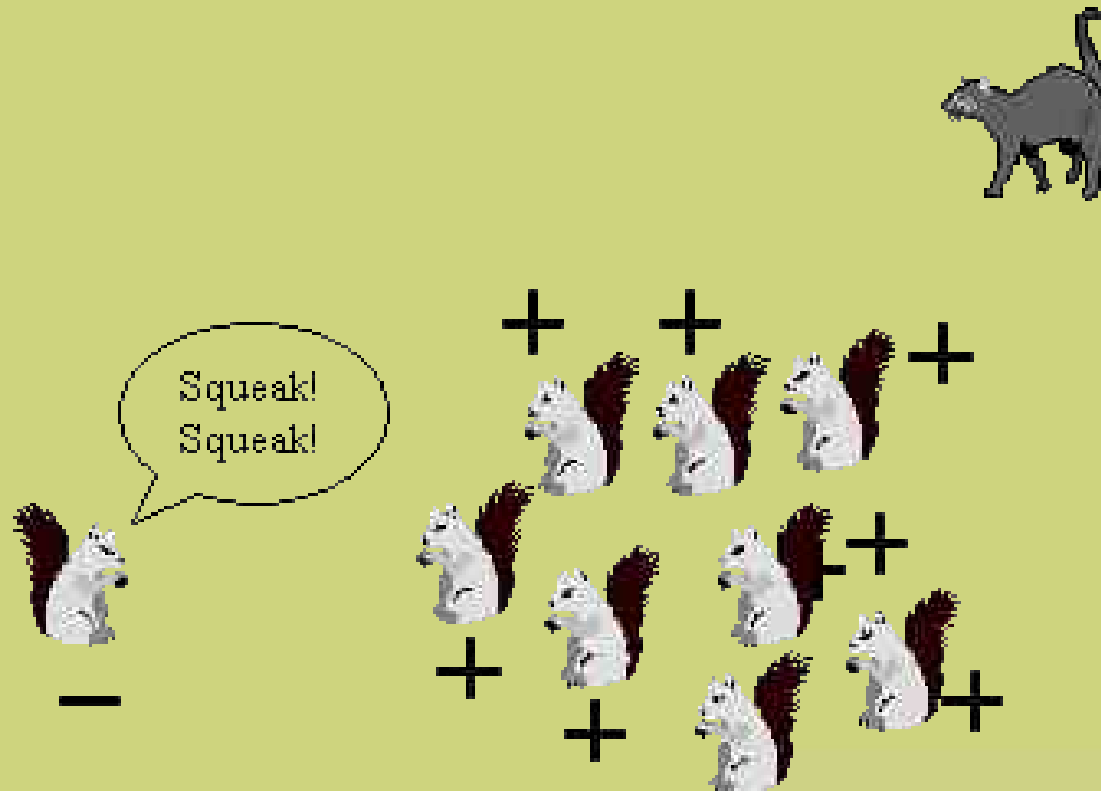
r = the genetic relatedness of the recipient to the actor

B = the additional reproductive benefit gained by the recipient of the altruistic act,

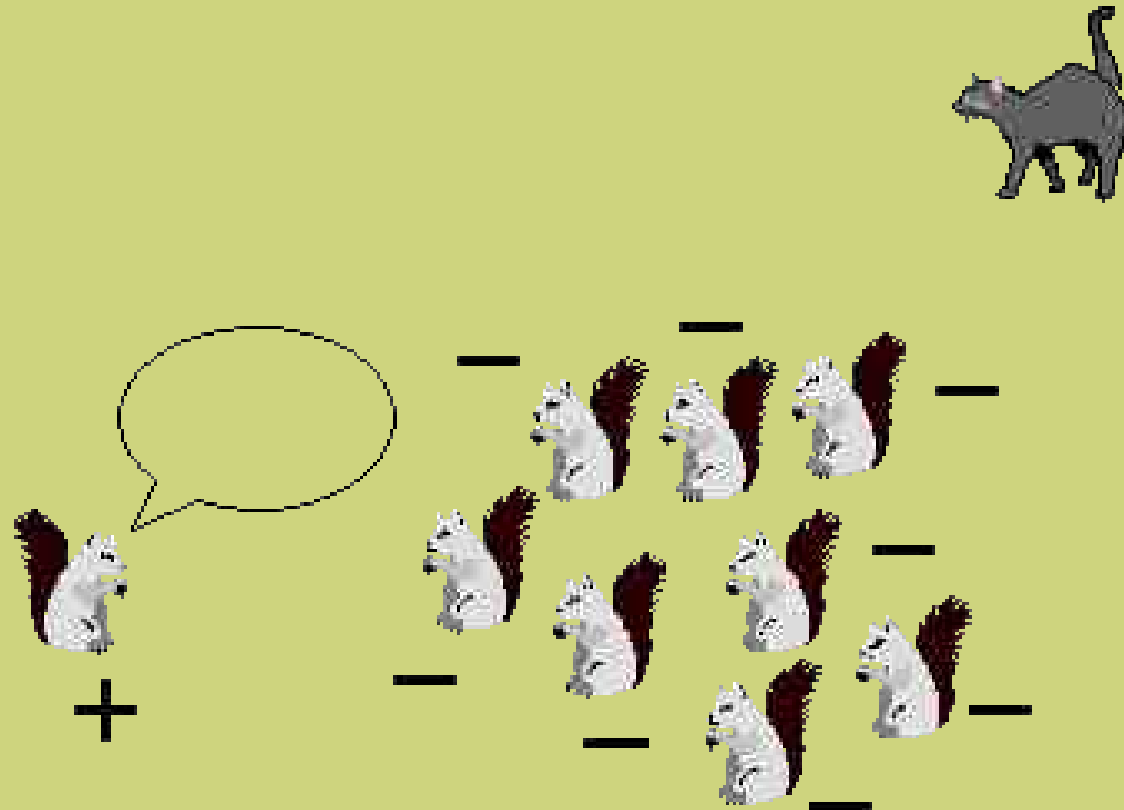
C = the reproductive cost to the individual of performing the act.

Example: alarm call

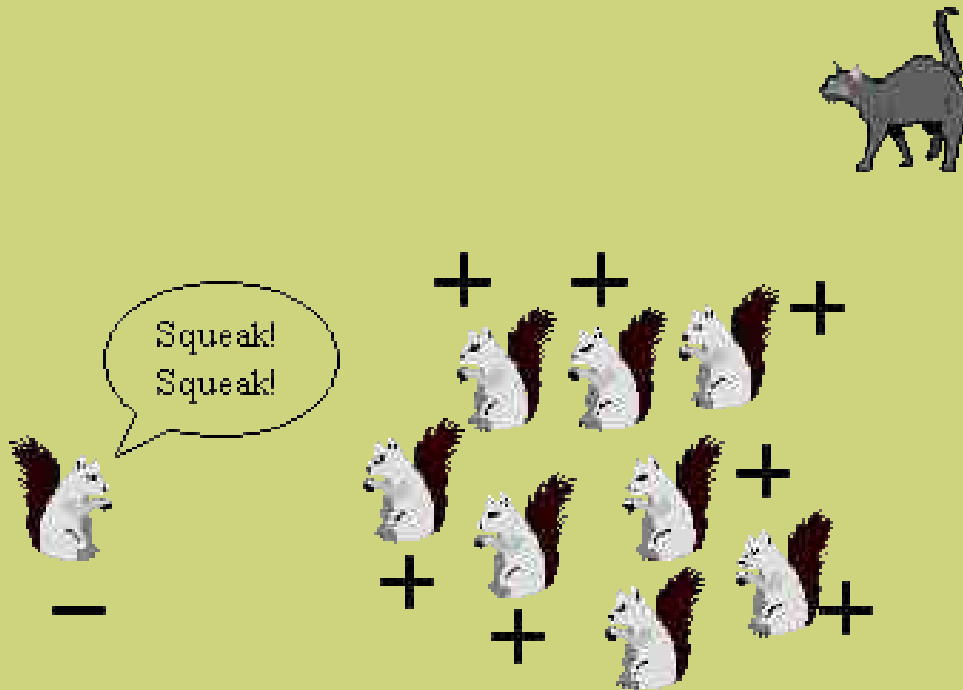
Caller is altruist (?)



Non-caller selfish



9 siblings in the group ($r = .05$)
cost of calling 0,3
benefit for siblings 0,1



$$c = 0,3$$

$$b = 0,1 * 8 = 0,8$$

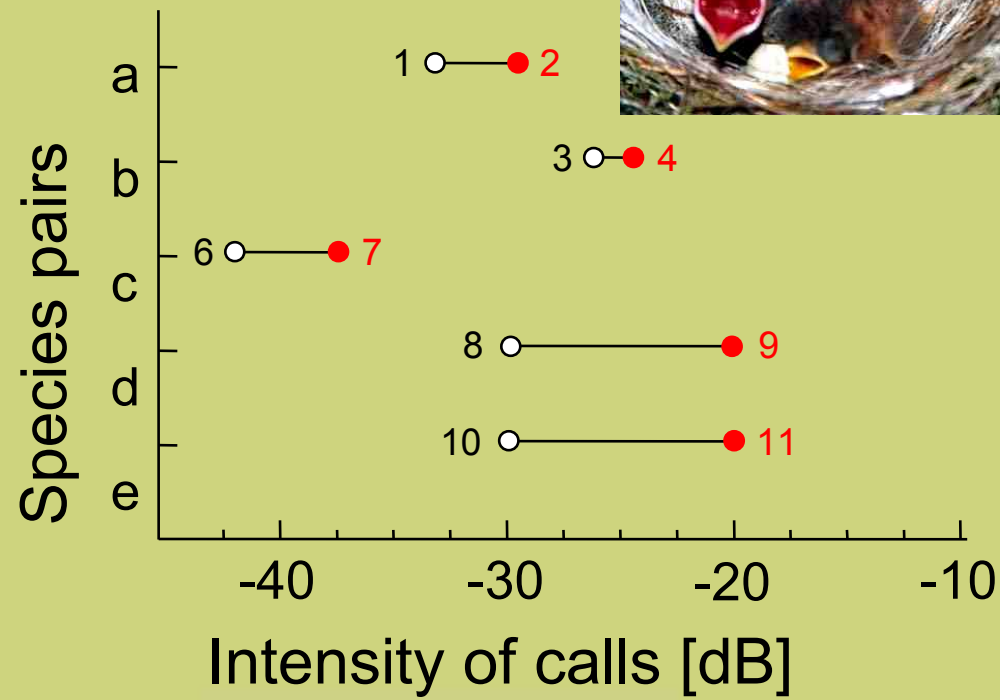
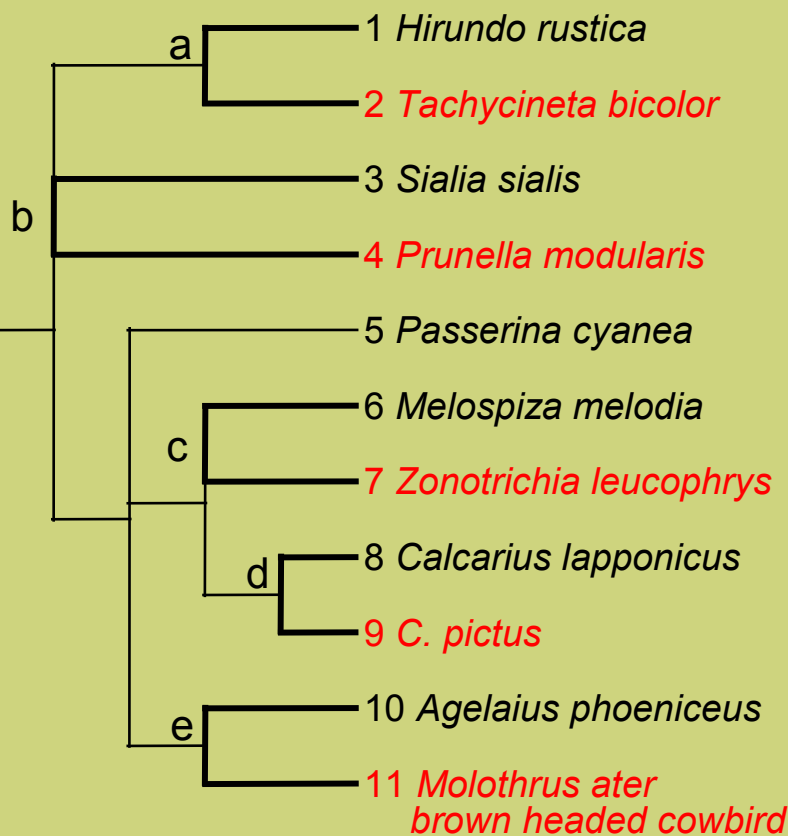
$$r = 0,5$$

$$rb = 0,5 * 0,8 = 0,4$$

Altruism stable, because $c < rb$ ($0,3 < 0,4$)

Degree of relatedness and begging

Begging call: beneficial for the actor, but increases predation risk
 lower relatedness -> higher competition



Lower relatedness, higher intensity

Black: high R (monogous)
 Red: lower R (EPC vasy intraspecific nest parasitism)

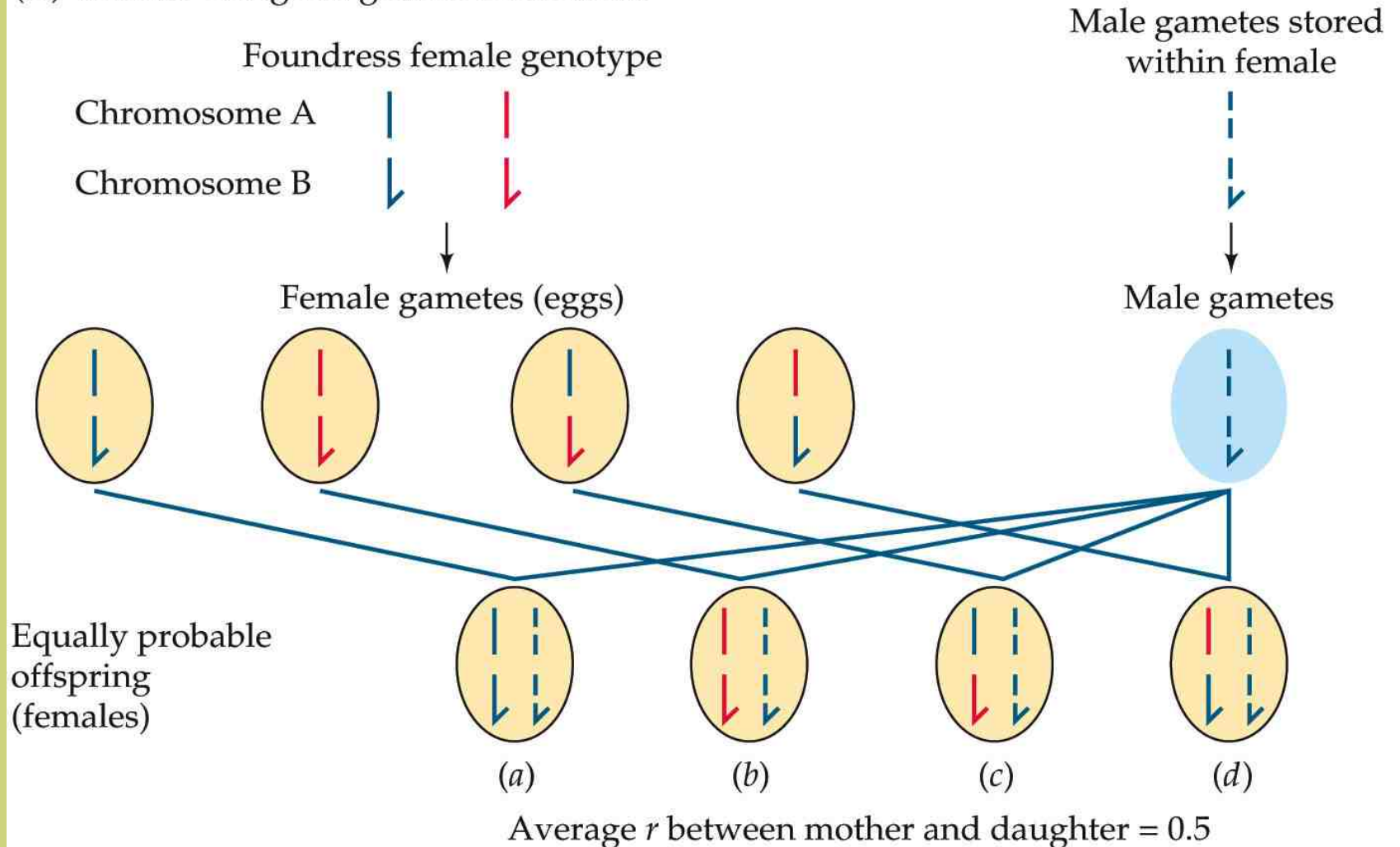
Begging Intensity of Nestling Birds Varies with Sibling Relatedness

Briskie et al. (1994) Roy Soc Proc

Begging for food is one of the most conspicuous behaviours performed by nestling birds. Recent models suggest that the form and **intensity of begging** evolved not only to communicate nutritional requirements to parents but also as a **mechanism for competing against siblings** to obtain a greater share of parental resources. In an interspecific comparison of passerine birds, we show that the loudness of nestling begging calls increases as the relatedness amongst the members of a brood declines. Species with high levels of mixed parentage, as well as the brood-parasitic brown-headed cowbird (*Molothrus ater*), begged louder than their closest monogamous and non-parasitic relatives. These results support the hypothesis that sibling relatedness influences begging behaviour in birds, and suggests that increased intensity of begging can evolve whenever female promiscuity or brood parasitism lowers the coefficient of relatedness among nestmates.

Haplodiploidy and the evolution of eusociality in the Hymenoptera According to Hamilton

(A) Mother–daughter genetic relatedness



Haplodiploidy and eusociality

Haplodiploidy explains the origin of eusociality under certain restrictive conditions:

when colonies produce much more females than males
(brothers are related to worker females by $r = 0.25$)

when workers keep on producing some of their own sons
($r = 0.5$)

Test of the haplodiploidy hypothesis: how many times did eusociality arise in haplodiploid vs. diploid groups?

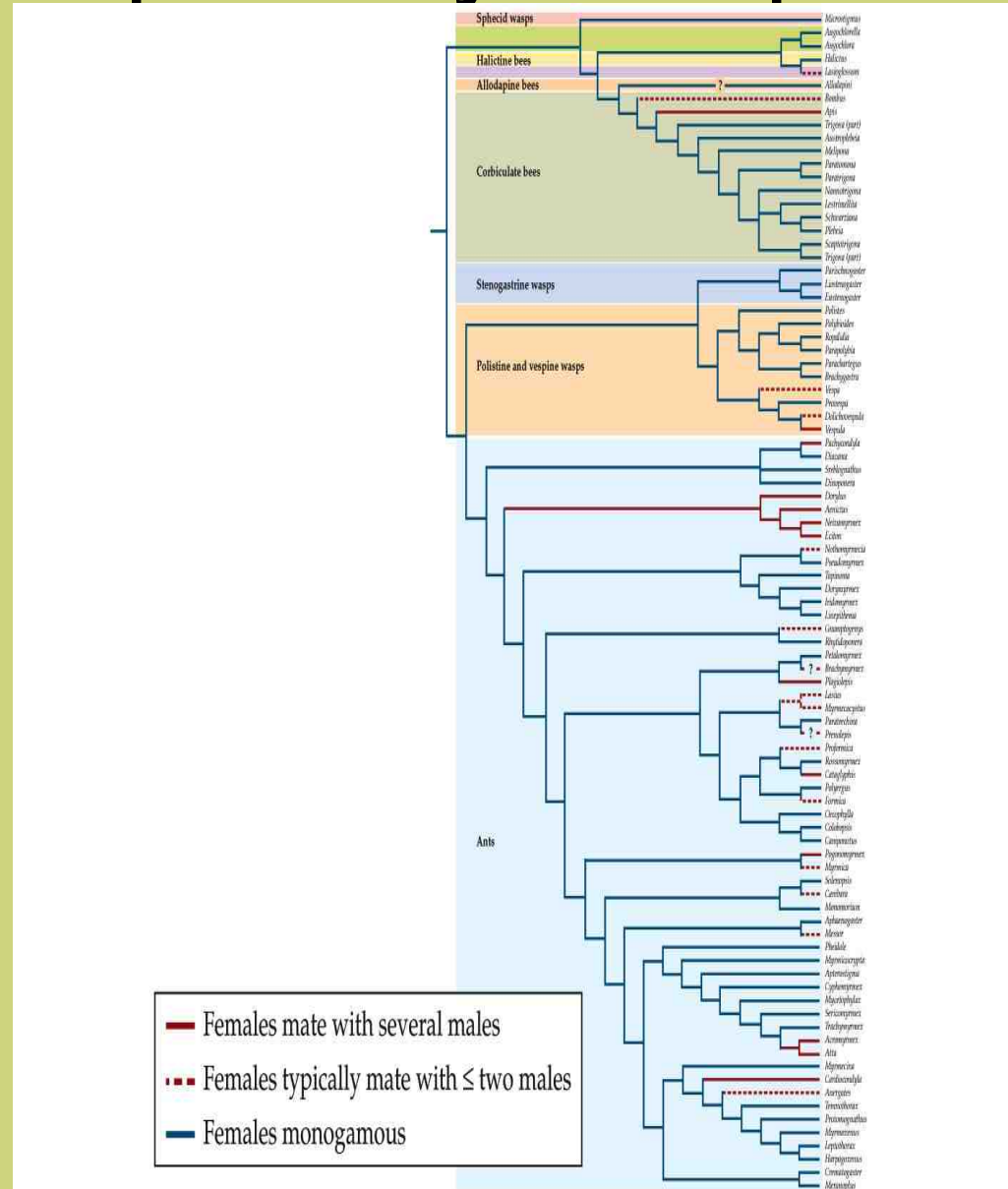
11 x in the haplodiploid Hymenoptera

1 x in ants

1 x in Vespidae wasps

1 x in Sphecid wasps

8 x in bees





3 x in haplodiploid
gall-forming thrips
„thunderbugs”

In Australia
cca. 1 mm long



foundress

soldier

2 x in diploid mole rats



Naked mole rat

Low genetic variation was found → inbreeding was assumed as explanation for eusociality

However, most samples came from one area where colonies went through bottleneck

Braude (1999)



Damaraland mole rat

Obligate outbreeder

In both species nonbreeder females are physiologically suppressed by the queen.

These

extreme (but reversible) reproductive blocks are brought about by social contact with the dominant breeding queen

Faulkes and Bennett (2001)

Number of origins of eusociality

Group	Genetic structure		
	haplodiploid	clonal	diplodiploid
Sociale Hymenoptera	11		
Thrips	2		
Aphids		5	
Termites			2
Beetles			1
Crustacea		(Shrimps)	3
Mammals			2
Total	13	5	8

Haplodiploidy or inbreeding

Haplodiploidy does not explain the origin of eusociality

Harsh environment, patchy distribution of food, high predatory pressure etc. → communal breeding → competition for breeding within colony → suppression of breeding → casts

Hamilton's rule: $B * r > C$