

Chapter 14

The Evolution of Social Behavior
(2nd lecture)

Social behavior is the exception, not the rule, in most taxa of animals. Why?

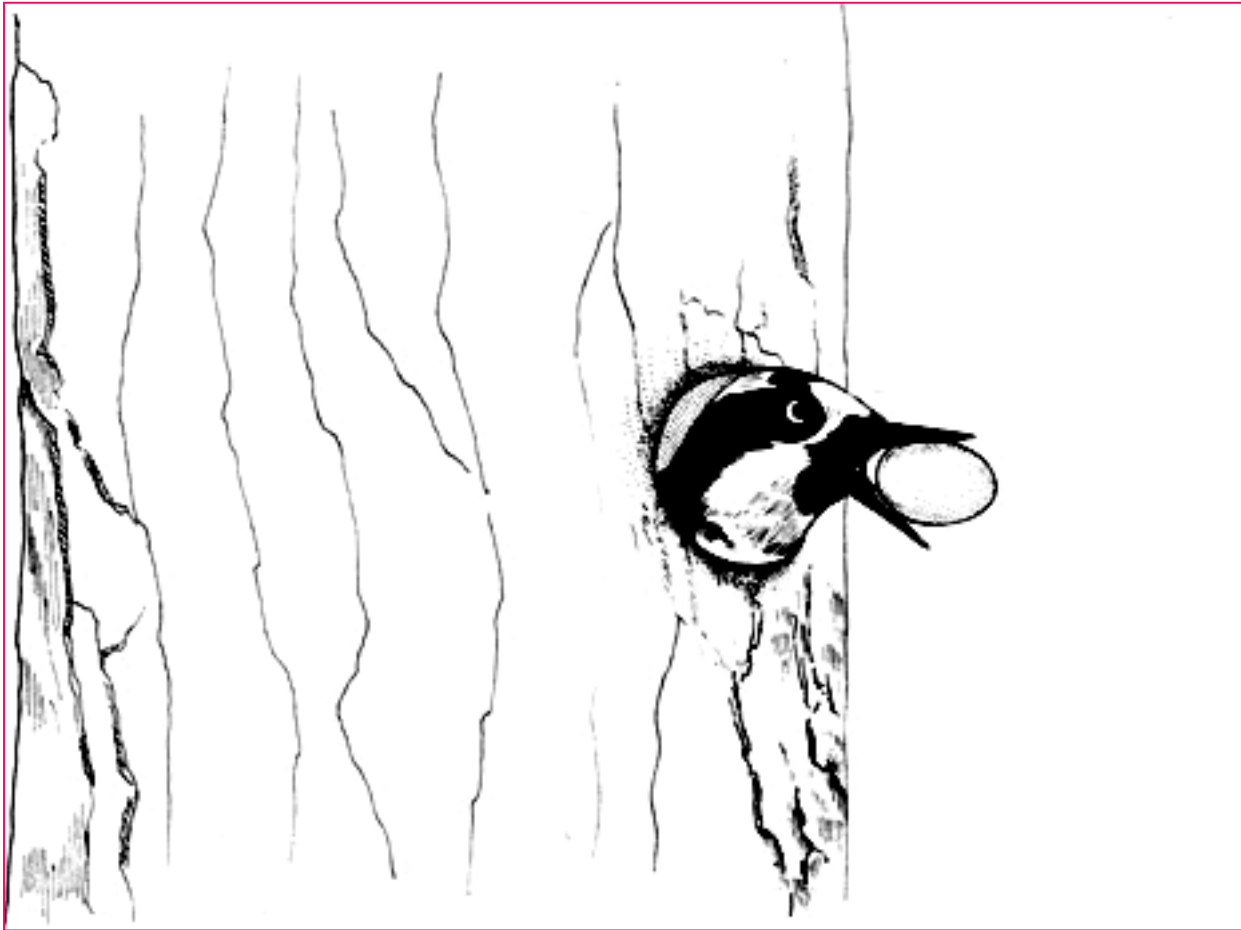
BENEFITS

- Reduction in predator pressure by improved detection or repulsion of enemies
- Improved foraging efficiency for large game or clumped ephemeral food resources
- Improved defense of limited resources (space, food) against other groups of conspecific intruders
- Improved care of offspring through communal feeding and protection

COSTS

- Increased competition within the group for food, mates, nest sites, nest materials, or other limited resources
- Increased risk of infection by contagious diseases and parasites
- Increased risk of exploitation of parental care by conspecifics
- Increased risk that conspecifics will kill one's progeny

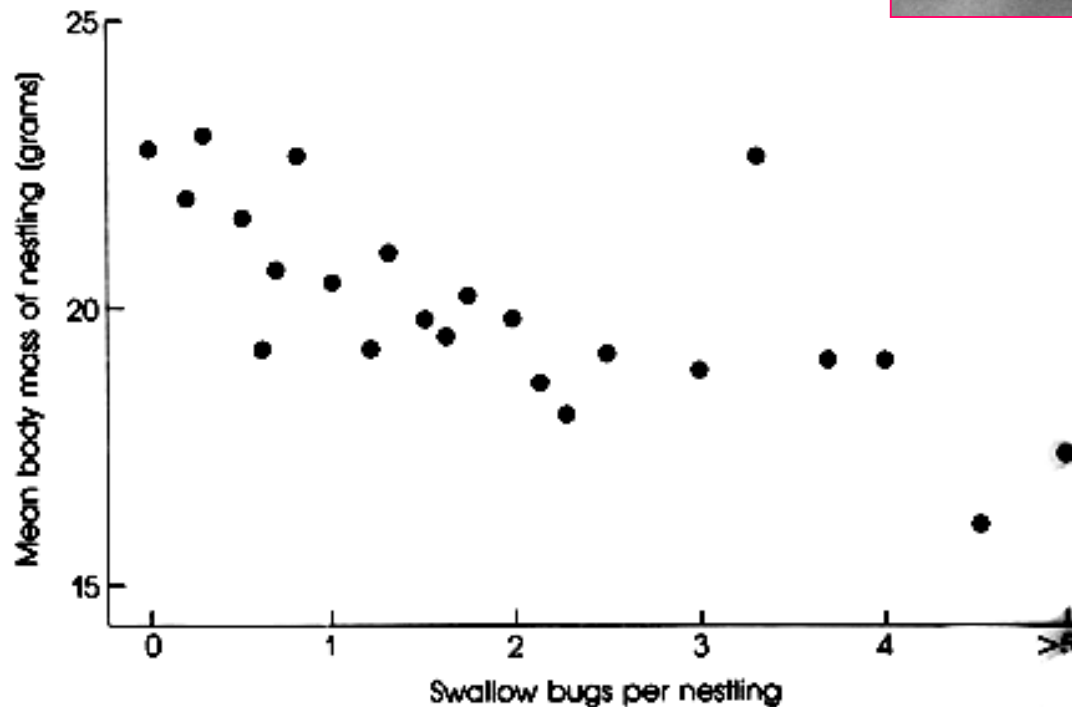
The costs of sociality include reproductive interference



Here one member of a breeding group of acorn woodpeckers removes an egg of a companion female from their communal nest

Effect of ectoparasites on cliff swallow nestlings

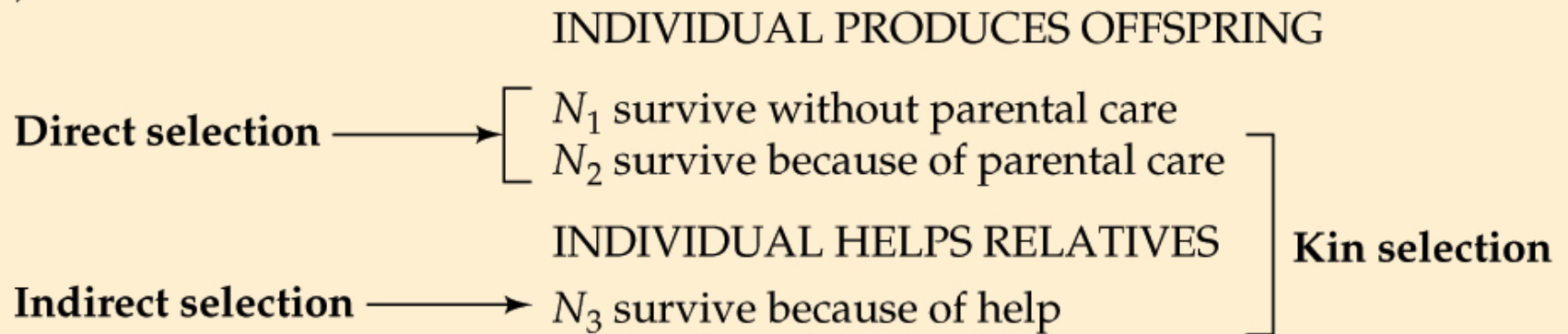
The big nestling on the right comes from an insecticide-treated nest; the stunted nestling on the left occupied a parasite-infested nest



In large colonies of cliff swallows, there are more swallow bug parasites per nestling. The more parasites per nestling, the less the nestling weighs.

How can individuals in a social group improve their fitness?

(A)



(B)

$$\left. \begin{array}{l} \text{Direct fitness} = (N_1 \times r) + (N_2 \times r) \\ \text{Indirect fitness} = N_3 \times r \end{array} \right\} \rightarrow \text{Inclusive fitness}$$

Inclusive fitness: the total genetic contribution of an individual to the next generation
 r = coefficient of relatedness (e.g., r of a human parent to each of its children is 0.5)
 N = number of offspring

Cooperation among scrub jay relatives



Helpers at the nest (i.e., unfledged young) in the Florida scrub jay provide food for the young, defense for the territory, and protection against snakes

Effect of helpers on reproductive success in Florida scrub jays

Year	Number of Pairs		Fledglings per Pair ($\bar{x}$)	
	Without Helper	With Helper	Without Helper	With Helper
1969	2	5	0	2.6
1970	8	8	2.0	3.5
1971	6	19	1.3	2.1
1972	13	17	0.3	1.6
1973	18	10	1.3	1.8

How could we estimate the inclusive fitness of a helper in 1969, assuming the coefficient of relatedness of helper to offspring (r) = 0.32?

Inclusive fitness = direct fitness + indirect fitness

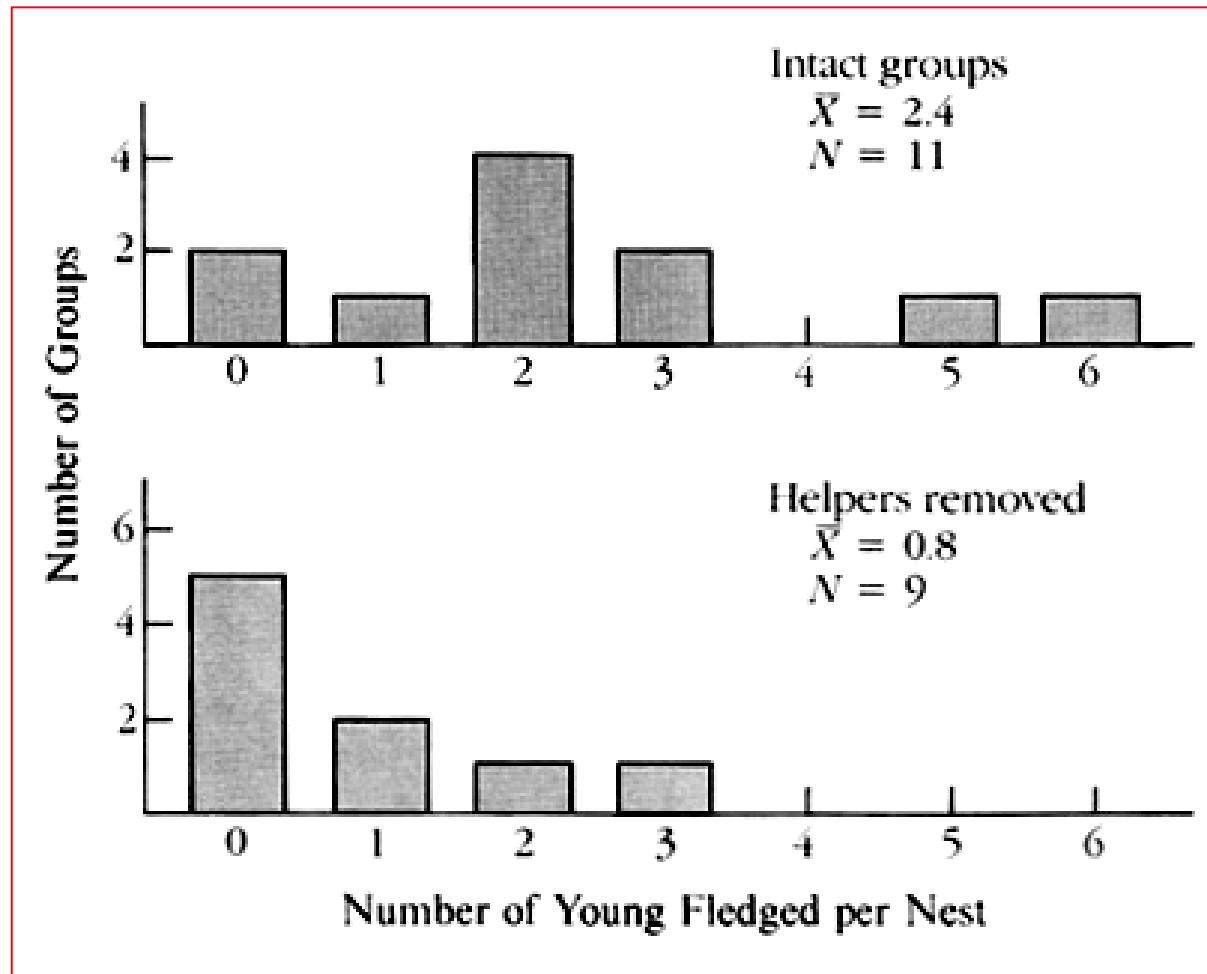
Direct fitness of helper = 0

Indirect fitness of helper = $(N_1 \times r) = (2.6 \times 0.32) = 0.83$

How would you estimate the direct fitness of each parent?

$(2.6 \times 0.5) = 1.3$

Effect of artificial removal of helpers on reproductive success in groups of gray-crowned babblers



Alarm call of a Belding ground squirrel that has spotted
a terrestrial predator like a coyote



This call causes other squirrels to rush for safety.
Is this an example of cooperation, or is it altruism?

What is the functional significance of the ground squirrel's alarm call?

Direct selection hypothesis: The caller enhances its personal chances for reproductive success by giving the alarm signal in several possible ways:

Predator confusion hypothesis: simultaneous flight of all squirrels confuses predator, helping the caller escape

Predator deterrence hypothesis: once the predator learns that it has been spotted, it will terminate the hunt to avoid wasting energy

Parental care hypothesis: a caller gives the signal to warn its offspring, increasing their chances of survival and thus the caller's direct genetic contribution to subsequent generations

Indirect selection hypothesis: Even though the caller reduces its lifetime reproductive success by sounding the alarm, it nevertheless raises its own inclusive fitness. All relatives are alerted by the signal, and the gain in indirect fitness outweighs the loss in direct fitness paid by the altruist.

Paul Sherman tested all of these hypotheses

He was able to reject the Predator confusion hypothesis and Predator deterrence hypothesis by showing that terrestrial predators are not confused by fleeing squirrels or deterred from continuing their attack. In fact, coyotes, weasels, and badgers attacked and killed the callers at a higher rate than they did the non-calling ground squirrels.

This leaves us with the *Parental care* and *Altruism* hypotheses, both of which predict that females would be more likely than males to give risky alarm calls.

This is because female Belding's ground squirrels tend to be sedentary, causing most females to live with her daughters and relatives. Males, on the other hand, move away from their natal burrow, and thus do not live near offspring or relatives that they may help.

Sherman found that females were more likely to give the alarm call when female relatives were nearby.
In addition, females were more likely than males to give the alarm call

Who gives alarm calls among Belding's ground squirrels?

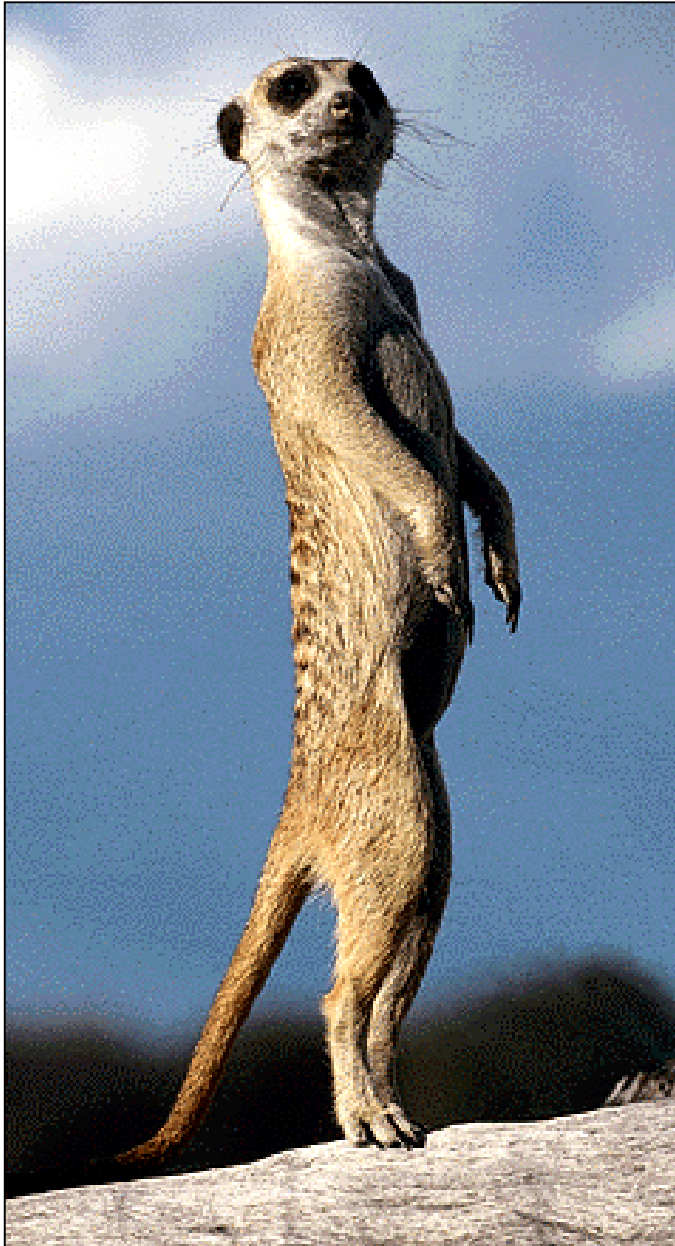
Category of squirrel	Exposures to predator ^a	Squirrels giving alarm call (%)	Squirrels expected to call if alarms are random (%)
Males >1 year old	67	12 (18)	19 (28)
Females >1 year old with living relatives ^b	190	75 (39)	53 (28)
Females >1 year old without living relatives	168	31 (18)	46 (28)

Source: Sherman, unpublished data.

^aNumber of times ground squirrels in each category were present when a terrestrial predator appeared 1974–1979.

^bRelatives consist of daughters, granddaughters, mothers, or sisters.

These data support the *Parental care* and *Altruism* hypotheses because females would gain direct fitness by helping their offspring to escape from predators, and indirect fitness to the extent that aunts and nieces and sisters escape as well.



In a variety of social birds and mammals, certain individuals act as guards while others forage for food. In some species, individuals trade-off sentinel duties in a coordinated fashion, perhaps to spread the danger evenly because guards are believed to be exposed to a greater risk of predation. What selection processes could explain the existence of such a potentially risky behavior in a large number of unrelated species?

A sentinel meerkat (*Suricata suricatta*) watching out for predators

The popular view has been that sentinel behavior evolved as a result of kin selection--that is, individuals tend to engage in behavior that benefits their relatives.

But, in a recent study, Clutton-Brock and colleagues show that sentinel behavior is a selfish, not a selfless, activity.



Meerkats commonly forage up to 20 cm Below the surface to locate invertebrates. During this time, they cannot look for predators, except by stopping and glancing around.



Clutton-Brock made the following observations

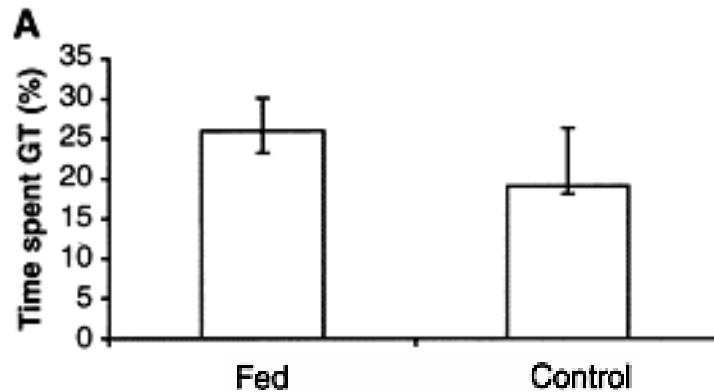
Meerkats did not suffer increased predation risk by exhibiting sentinel behavior

All meerkats benefited from early warnings by sentinels

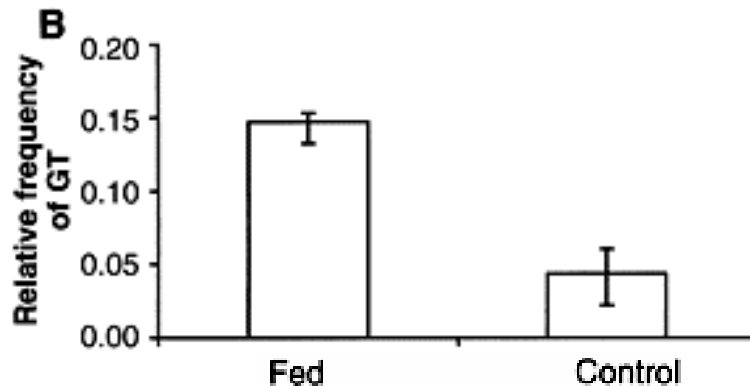
Meerkats did not exhibit the sentinel behavior more often when in close proximity to relatives

Thus, the functional explanation for the meerkat sentinel behavior must be different from that of the the Belding's ground squirrel alarm call

Are the meerkats with a full stomach more likely to exhibit the sentinel behavior?



Total time spent in the raised guarding (GT) posture by meerkats after they had been fed 25 g of hard-boiled eggs (fed) versus the same meerkats after no feeding (control)



Frequency at which fed and control meerkats exhibited raised guarding over a 30-day period

These data indicate that meerkats are literally “looking out” for their own best interests, when their nutritional status permits them to do so

What generalizations can you draw from the ground squirrel
and meerkat studies?