Behavioral Ecology of Vertebrates

Unit 12. Cooperation

Module 5 Cooperation

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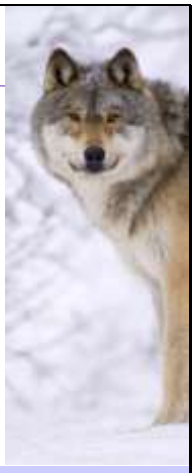


Learning, Discovering and Sharing Knowledge

In the previous module, we looked at how social relations influence reproductive success of relatives. In this module, we expand that circle to ask whether there are mutual benefits for actors who are not related and may actually be different species. To put this unit in the context of this last module 5 of our course, we will examine communication next (Unit 13) and finish up with a concluding chapter about what this all means for field studies (Unit 14).

Learning Objectives (Davies et al. 2012:144)

Cooperation: "fitness benefits" for actor & receiver

1. **Theoretical framework:** nested levels of selection influence variation of genotypes in gene pools

   (((individual) kin) population)

2. **Indirect benefits:** apparently "altruistic", helping relatives with similar genes, cooperative breeding
3. **Direct benefits:** mutually beneficial (reproduction &/or survival), by-product mutualism, reciprocity, enforcement

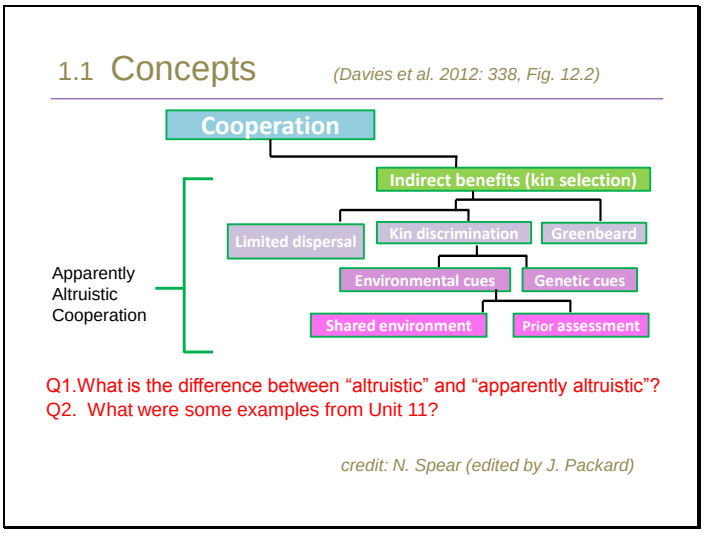
In the last unit 11, we clarified what is meant by kin selection. This reinforced the idea that natural selection edits genotypes. Those genotypes may change in % due to lifetime reproductive success of individuals or their kin who carry the same genotype. We also learned from examples of bacteria that the % genotypes can shift in different ways in different populations. However, we left it a open question how evolutionary biologists view natural selection at individual, kin and population levels of the biological hierarchy. These processes are not mutually exclusive. They may be additive or contradictory or neutral. So I want to start with the theoretical framework, then move on to examine more studies that clarify the interaction of indirect and direct benefits in the complex interactions categorized as cooperative.

Davies et al. 2012, Fig 12.6

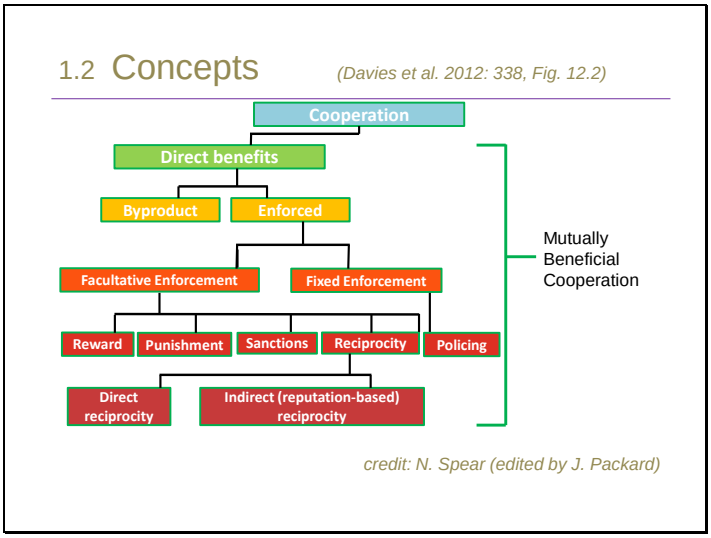
Is there a genetic basis for cooperation?

1. Theoretical framework

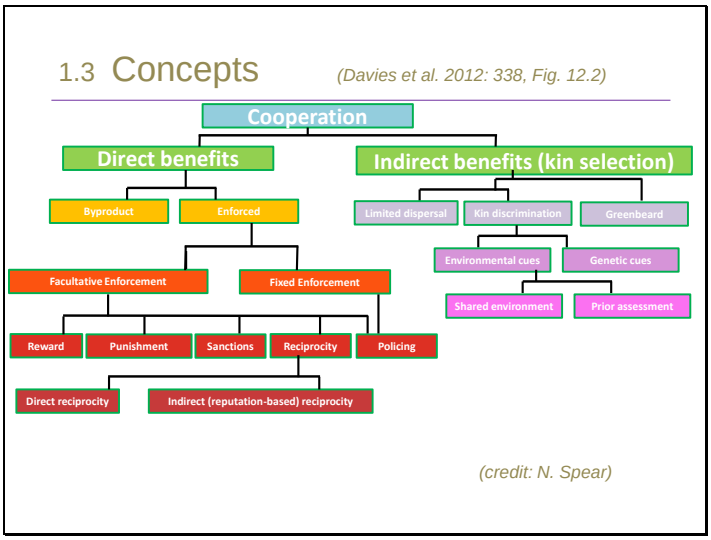
Tantalizing question…if the animal nature of humans is basically selfish, then that has alarming implications for society. If there are genetic pre-cursors to cooperation in other animals, does it give us more hope as humans?



-Kin selection explains altruistic cooperation between relatives, which helps increase a trait's genetic representation in future generations.
-The greenbeard example is from chapter 11– the idea that there may be recognition alleles which express phenotypically, resulting in those with the allele to behave altruistically to others who also have these alleles.



These classifications are but one way to categorize types of cooperation.
When interactions are between non-relatives, clearly the benefits are direct (reproduction or survival), not indirect benefits through reproduction of kin.



Over the last few decades, the literature on cooperation has expanded enormously. This is partly because different models apply to different taxonomic groups. The subtleties of the models and alternative working hypotheses are sometimes hard to follow. This figure provides a good road map if you are interested in picking a model that applies to the organism you are studying. For vertebrates, by-product mutualism, enforcement, and kin discrimination seem to be the ones that are now gaining the most attention in the literature. This theoretical basis is much more relevant for the study of invertebrates. For those of you interested in invertebrates, I encourage you to read Chapter 13. There are actually a couple of good examples of vertebrates in that chapter, which used to be in this chapter (naked mole rats, bee-eaters). However, remember we will be skipping Chapt 13 and move onto Chapt 14 for Unit 13.

1.4 Poll- lets see if you understand

About which topics would you like to chat more?

a) Cooperation related to indirect benefits
b) "Altruism" vs. "apparent altruism"
c) Cooperation related to direct benefits
d) Nested hierarchy of selection
(((individual) kin) population)
e) I'm good, let's move on

Davies et al. 2012, Fig 12.1

Cooperation among relatives

2. INDIRECT BENEFITS

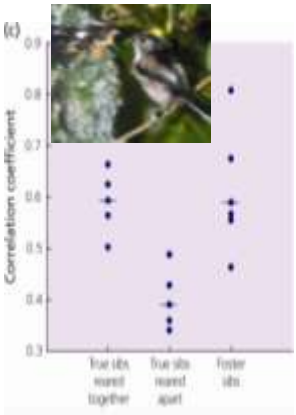
2.1 Kin- recognition (learned)

(Davies et al. 2012: Fig. 12.3)

Long-tailed tit "churr" calls
- given frequently by both sexes
- short-range communication
- nest building & aggression

Hyp: Kin recognition sign

Test: genetic & environmental influences on development
- Switched eggs from different nests
- "Foster" siblings more similar to nest mates than to relatives
- True sibs reared apart were less similar



credit: T. Harrington (edited by J. Packard)

(Sharp et al 2005); Hypothesis: The calls of relatives should be more similar. They took eggs from different nests and switched them. Foster Siblings – unrelated individuals reared in the same nest

"Foster" siblings developed churr calls more similar to the calls of those they had been raised with rather than those who they were most genetically related to.

2.2 Helping kin

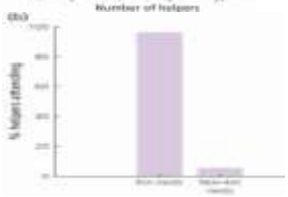
(Davies et al. 2012: 340, Fig. 12.3)

Long-tailed tits

- High rate of nest predation
- Failed breeders helped relatives
- 79% of 52 helpers were closely related to the breeders
- Number of helpers per nest correlated with offspring survival
- Helpers die over winter

Choice test: Kin Discrimination

- Failed nest equidistant between "kin" and "non-kin" nests
- individuals chose to help the "kin" in 16 of 17 cases



Why is this evidence for indirect benefits being more important than direct benefits?

credit: T. Harrington (edited by J. Packard)

-Observed tits that didn't breed help others who had chicks

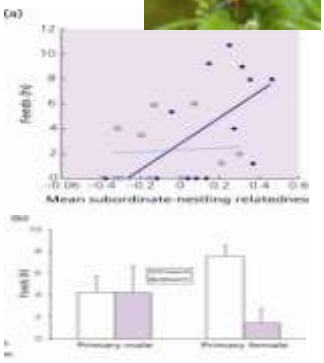
-Put non-breeding individuals equidistant from a nest with relatives and one with non-relatives

-An analysis of the long term data suggested that indirect fitness benefits are the major reason for this helping behavior
Long-tailed tits (Russell and Hatchwell 2011) Gathered observational data from 52 helpers finding that 79% of helpers were closely related to the breeders. An increase in the number of helpers per nest showed an increase in offspring survival

They went on to test for Kin Discrimination. In choosing between kin and non-kin nests 16 out of 17 trials showed that individuals chose to help the nest with relatives

2.3 Helping kin (Davies et al. 2012, Fig 2.11)

- Seychelles warbler
- Habitat saturation
  - Effective conservation
  - Translocated to islands
- Feeding correlated with relatedness?
  - Males- NO (circles)
  - Females- YES (dots)
- Females more likely to help "mother"



2.4 Poll- lets see if you understand

Premise for debate: "Helping at the nest is '*apparently altruistic*' cooperation because parents gain direct benefits but their helping kin do not"

a) I agree
b) I disagree
c) It depends

Lets dialogue more about this using the elearning discussion tool


Davies et al. 2012 Fig. 12.5

Cooperation independent of relatedness

3. DIRECT BENEFITS

Studies of cooperative breeding usually investigate a mix of indirect and direct benefits. Obviously, when individuals are not related, then kinship selection would not be a relevant hypothesis. Alternative hypotheses include by-product mutualism and enforcement. Previous hypotheses related to reciprocity have been criticized by Clutton-Brock and are not even addressed in this chapter.

3.1 By-product benefits *(Davies et al. 2012: Fig. 12.5)*

Meerkat groups < 20

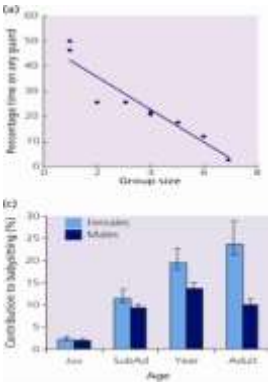
- Breeding pair
- Offspring (both sexes)
- Immigrants (mostly males)

Success depends on babysitters

- Feed & guard young at burrow
- Rest of group forages
- Lose 11% of body weight

By-product of large group

- Predator vigilance
- Defend territory
- Lower mortality
- Inherit breeding position



The hypothesis of by-product mutualism is that all members of the group benefit from the advantages of group life. The meerkats are given as an example. However, lets apply critical thinking.

3.2 Enforcement- Meerkats *(Davies et al. 2012: Fig. 12.8)*

Dominant females evict subordinates

- increased survival rate for the dominants offspring (infanticide by subordinates if not evicted)
- reduced competition for offspring

Evicted pregnant subordinate females

- older & less related
- high stress hormone metabolites (fecal)
- higher rate of abortion
- decline in body weight

How is this evidence for direct cooperation?


credit: J. Cantwell
(edited by J. Packard)

In the discussion, may want to mention how this relates to enforcement.
The meerkat example is enforced cooperation via harassment.

3.3 Enforcement *(Davies et al. 2012: 354, Fig. 12.9)*

Cleaner fish *Labroides dimidiatus*

- Removes and consumes ectoparasites from host fish
- Prefers mucus and tissue from hosts
  - Costly to host
  - Host chases or flees (punishment)
  - Cleaner changes feeding behavior

(credit: J. Carbaugh)

So the previous example may be ambiguous between it is not clear what is the relatedness between babysitters and breeders. Lets look at an example where the individuals who both benefit clearly do not share genes in common, because they are different species.

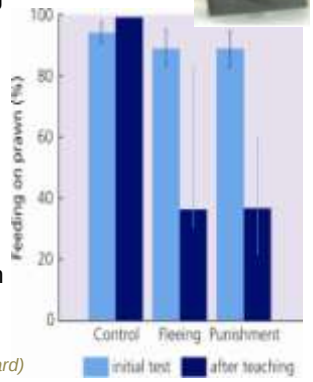
3.4 Enforcement *(Davies et al. 2012: 354, Fig. 12.9)*

Experiment simulating feeding opportunities for cleaner

- Fed on prawn (preferred) and fish flakes from plates
- "Client Flight": removed prawn plate (negative reinforcement)
- "Client Fight back": chased cleaner with plate (punishment)

Result: Cleaner learned from the consequences of its action

Q: Why is this evidence for direct cooperation?



credit: J. Carbaugh (edited by J. Packard)

Is this cooperation? Or is it simply a learned foraging behavior? Do we have any evidence about the genetic benefits (survival and reproduction)?

3.5 Hidden Benefits *(Davies et al. 2012: 341, Fig. 12.4)*

Superb Fairy-wren in Australia

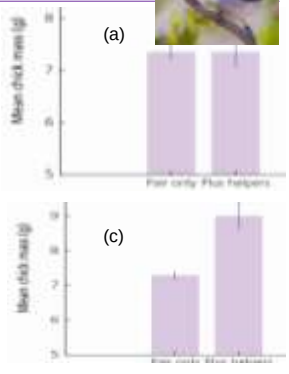
- Cooperative breeding
- No short-term direct benefits (a)
- Variation in egg size

Hypothesis: direct benefits for breeders are long-term survival

Cross-fostering experiment (c)

- Controlled for variation in egg size
- Moved same-size eggs to nests
- Larger chicks in nests with helpers

Q: What is meant by "hidden benefits"?



credit: F. Cartaya (edited by J. Packard)

Russell et al., 2007 Study "a" showed no difference in mean chick size with the aid of helpers. No fitness benefits of helpers

Cross-fostering experiment "c" of moving same size eggs to nests with helpers showed increase in chick size

3.6 Hidden Benefits *(Davies et al. 2012: 341-342, Fig. 12.4)*

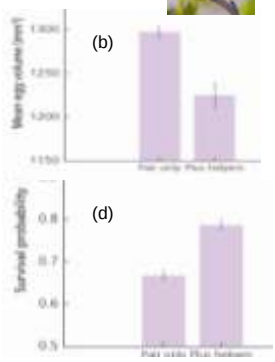
Variation in egg volume related to helpers

- Females with helpers laid smaller eggs
- "reduced costs" (b)

Long-term benefits (16-year data collection) breeding pairs with helpers had increased survival in the next season (d)

- Hypothesis 1: Helpers increase competition for food resources
- Hypothesis 2: Females with helpers invest in less reproduction effort

Take Home message: Though indirect benefits may be short-term, direct benefits to breeders were long-term (increased survival for breeders)



credit: F. Cartaya (edited by J. Packard)

Study "b" showed decrease in egg volume from low reproductive activity and low investment to egg provisioning from female.

16 year data collection "d" showed that breeding pairs with helpers led to an increase survival probability for breeders for the next season

Possibility 1: Helpers increase competition for food resources

Possibility 2: Females with helpers invest in less reproduction effort

Take Home message: Though benefits to individual helpers and breeders may be short term, long tern benefits from helpers will increase survival for breeders for nest season

3.7 Poll- lets see if you understand

Premise for debate: "Although we have evidence for cooperation in the proximate sense, there is little evidence for cooperation between non-kin in the ultimate sense"

a) I agree
b) I disagree
c) It depends

Depends on: (1) time frame, (2) scale of area, (3) which species. Missing: ecological saturation model; hard times model. Lets dialogue more about this using the elearning discussion tool

Summary (Davies et al. 2012 Chapt 12)

1. **Theoretical framework:** nested levels of selection influence variation of genotypes in gene pools

   (((individual) kin) population)

2. **Indirect benefits:** apparently "altruistic", helping relatives with similar genes, cooperative breeding

3. **Direct benefits:** mutually beneficial (reproduction &/or survival), by-product mutualism, reciprocity, enforcement

In this webinar, I have tried to reinforce the idea that natural selection edits genotypes. Those genotypes may change in % due to lifetime reproductive success of individuals or their kin who carry the same genotype. Evolutionary biologists view natural selection as occurring simultaneously at individual, kin and population levels of the biological hierarchy. These processes are not mutually exclusive. They may be additive or contradictory or neutral. We examine studies that clarified the interaction of indirect and direct benefits in the complex interactions categorized as cooperative. You learned the keyword concepts most relevant to vertebrates. Remember that we are skipping Chapter 13 on invertebrates, but I encourage you to read that if you are interested. Next unit we apply the ideas of mutual benefits to communication.