Behavioral Ecology of Vertebrates

Unit 11. Altruism/Spite

Module 4 Reproduction

j-packard@tamu.edu

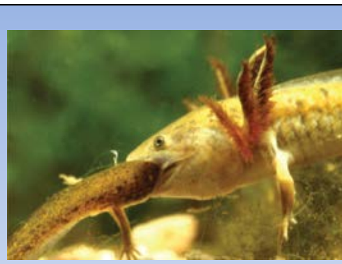
Learning, Discovering and Sharing Knowledge

Last unit, we recognized that social group living influences the clumping of females, a key factor in mating systems. In module 3 we learned about the benefits of living in groups, but we did not specify whether the individuals in the group were related or not. In this unit, we focus on how the social interactions among relatives may influence the growth and survival of their young. In this presentation, I have made choices that emphasize implications for reproductive behavior rather than the complex theories associated with evolution of cooperative behaviors. We will examine that topic in the next module.

Learning Objectives (Davies et al. 2012:144)

1. **Interactions of relatives:** mutually beneficial, selfish, altruistic, spiteful
2. **Kin discrimination (proximate):** coefficient of relatedness, kin signal, kin recognition, care-giving directed preferentially to kin
3. **Kin selection (ultimate)**: inclusive fitness, Hamilton's rule, "green beard" effect, free riders

Although the textbook emphasizes theoretical aspects, in this webinar, we will focus on the practical aspects. Relatives matter in survival to reproductive age. Start with defining terms used in game theory, follow with proximate perspectives of actual behavior we can observe, then move on to the evolutionary models.



Pay-offs for actors and recipients

1. INTERACTIONS OF RELATIVES

Lets start with defining some of the terms that are used to categorize interactions between relatives. These are defined for the purpose of game theory models of evolution.

1.1 Interactions (Davies et al. 2012 Table 11.1)

PAYOFF TO ACTOR	PAYOFF TO RECIPIENT +	PAYOFF TO RECIPIENT -
+	Mutual benefit (cooperation)	selfish
-	altruistic	spiteful

In game theory, these are the technical terms used to describe interactions. When an interaction is beneficial to both the actor and the recipient, what would you call it? These are the types of interactions we will talk more about in the next module. In this module we will talk about interactions with negative payoffs. If the action benefits the recipient, but not the actor, what do we call it? Beneficial to actor but not recipient? If neither benefit?

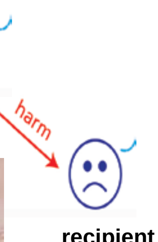
1.2 Selfish & altruistic (Davies et al. 2012 Fig. 11.2)

- Turkey- breeding tactics
  - Single breeder
  - Coalition breeder
  - Coalition non-breeder
- Brothers
  - form coalition before first breeding season
  - together until one dies
  - no switching
- Which tactic is altruistic? Selfish?

In actual relationships, an interaction may be altruistic from the perspective of one actor and selfish from the perspective of the other. This is one of the major sources of confusion. Turkeys are a good example.

1.3 Spiteful (Davies et al. 2012 Fig. 11.10)

- Both actor & recipient
  - Costs > benefits
  - Proximate sense
- What are some examples of spiteful behaviors?



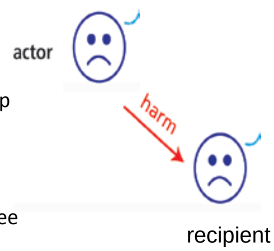
C. floridanum

We have few good examples of spiteful behaviors in vertebrates. If you find an example where spite is widespread and persists over many generations, I will nominate you for the Nobel Prize! Adaptationist thinking assumes it would not persist because it is not good for the species. We need to test the assumptions that spite would not persist, practicing critical thinking skills rather than blind acceptance of folk psychology.

Notice that I modified this diagram so both faces are frowning. In the proximate sense, by definition, an interaction is spiteful if neither the actor or recipient benefit. We will come back later to theories of how that might evolve in terms of the genetics.

1.4 Spiteful (Davies et al. 2012 Fig. 11.10, 11.11)

- Both actor & recipient
  - Costs > benefits
  - Proximate sense
- Examples
  - Sterile soldier parasitoid wasp eats siblings within a host caterpillar
  - Bacteriocin
  - Worker bee stings a robber bee and both die
  - Two roosters fight to the death



First two are examples from textbook. Last two are from experience.

1.5 Poll- lets see if you understand

Which of the following is an example of spite?

a) African painted dog kills her sisters pups
b) Stickleback fish eats eggs from another nest
c) Mountain sheep harasses injured male
d) Macaque infant interrupts mother’s copulation
e) Juvenile male & immigrant female ground squirrels kill infants

none


Davies et al. 2012, Fig 11.6

Relatives recognize and care for each other

2. KIN DISCRIMINATION

Next lets look at the three criteria used to determine whether kin might care for each other. Notice that this is an extension of parental care, directed toward individuals who are not actual offspring of the actor. These are the Belding’s ground squirrels that have been studied for their alarm calling behavior in response to a predator stimulus.

2.1 Kin discrimination *(Davies et al. 2012: 319, Fig. 11.3)*

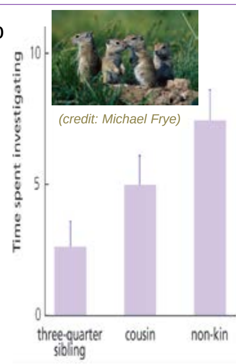
- Individuals can
  - Signal relatedness
  - Distinguish close kin from distant kin
  - Change their behavior accordingly
- Example: the *Gp*-9 locus in the fire ant *(Keller and Ross 1998)*
  - Workers with the *b* allele recruit newly mated queens, who express the same *b* allele
  - Any queens without the *b* allele are dismembered
  - What is the signal?

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

Three criteria for kin discrimination (proximate sense). Multi-queen colony; recognize members by odor. Remember this example for the next section where we discuss the "green beard" effect

2.2 Kin recognition *(Davies et al. 2012: 324, Fig. 11.6)*

- Belding's ground squirrels (Mateo 2002)
  - Live together in coteries (clusters of burrows)
  - Signal: odor cues
  - Distinguish between kin & non-kin: "Individuals spent more time investigating cubes which had been rubbed over closer relatives" (Davies et al. 2012: fig 11.6)
- Critique: Is this what the graph shows?

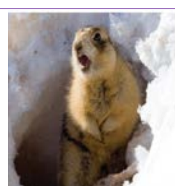


credit: J. Travis (edited by J. Packard)

What is meant by "investigating cubes"?
How was this tested?
Who wants to look up this reference and see whether it was mis-cited by Davies et al?

2.3 Alarm calls (Davies et al. 2012, Fig. 11.1)

- Black-tailed prairie dogs (Hoogland 1983, 1995)
  - Live in groups called coteries
  - By using a predator decoy data was obtained for alarm calls
- Alarm calls by individuals not associated with the main coterie
  - Are there "benefits" to one coterie making alarm calls to help a different coterie?
  - How would you test this?
  - Alternative hypotheses?

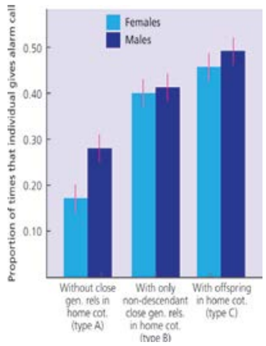


credit: T. Harrington (edited by J. Packard)

•By using a predator decoy data was obtained for alarm calls
•Note that alarm calls were still made by individuals who had no association with the main coterie.
- •This suggests that there could be benefits to one coterie making alarm calls to help a different coterie
- •It could reduce predation by having low predatory success in that area

2.4. Change behavior to kin (Davies et al. 2012 Fig 11.1)

- Prairie dog alarm calls least likely when no close genetic relatives were in the coterie
- individuals gave alarm calls just as frequently when there were non-descendant kin as when offspring were present
- When no close kin were present, how and why did the sexes differ?

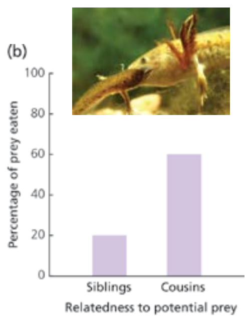


credit: T. Harrington (edited by J. Packard)

INTERESTING: prairie dogs distinguished between non-kin and kin; but they did not behave differently in the presence of close and distantly related kin.

2.5 Cannibalism (Davies et al. 2012, Fig. 11.9)

- Arizona tiger salamander
  - Morph A: eats invertebrates
  - Morph B: eats larval salamander
- Prediction: Cannibal morph B more likely to eat distant relatives
- Test kin recognition
  - Discriminators (detect sibs)
  - Non-discriminators (no detection)
- Test change in cannibal behavior
  - Discriminators ate 2 of 6 sibs
  - Non-discriminators ate 4 of 6 sibs



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

- Cannibalism – individuals eat others of the same species
- Pfennig and Collins (1993) tested if salamander larvae development into cannibalistic morphs was influenced by interaction with relatives or non-relatives
  - Ho: inclusive fitness theory suggests that cannibalism is less likely with relatives because that would cause a loss to indirect fitness
  - Larvae were reared in groups of 16 with either siblings or a mix of siblings and non-siblings
  - Results showed that larvae were less likely to develop into cannibals when reared with just siblings
  - INTERESTING: results also showed that in the mixed groups cannibals usually consumed non-siblings instead of siblings
- Pfennig went further and used Hamilton's rule to test the kin selection hypothesis
  - Using a variety of discriminators (avoid eating kin) and non-discriminators (show no preference) he showed that, even with the non-discriminators, a larger percentage of individuals eaten were not kin.

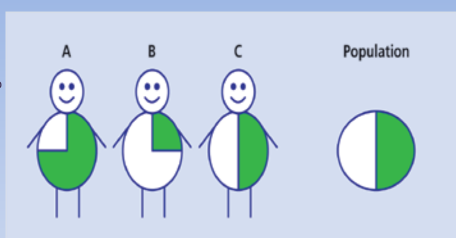
2.6 Poll- lets see if you understand

To test for kin discrimination, the following criteria are sufficient:

- Recognition of kin vs. non-kin
- Change in behavior directed to kin

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

(b). What is missing? Lets dialogue more about this using the elearning discussion tool



Davies et al. 2012 Fig. B11.5.1

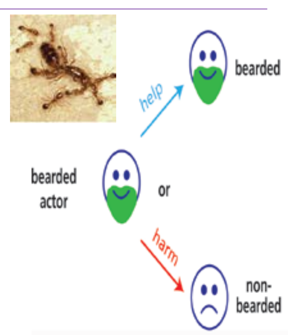
How could apparent altruism persist?

3. KIN SELECTION

Now for the ultimate perspective. Models that address the evolution of altruism are very complex. Technically, the criteria needed to actually detect kin selection are based on which genotypes are more likely to be shared by relatives than they are likely to be shared by members of the general population. Rarely do we have this evidence. So most textbooks resort to cartoons. My major take home message is “do not assume kin selection is an explanation until it has been tested”. Note this is a open critique of the textbook, which starts with the assumption that all behavior is adaptive.

3.1 Kin selection *(Davies et al. 2012: 319, Fig. 11.3)*

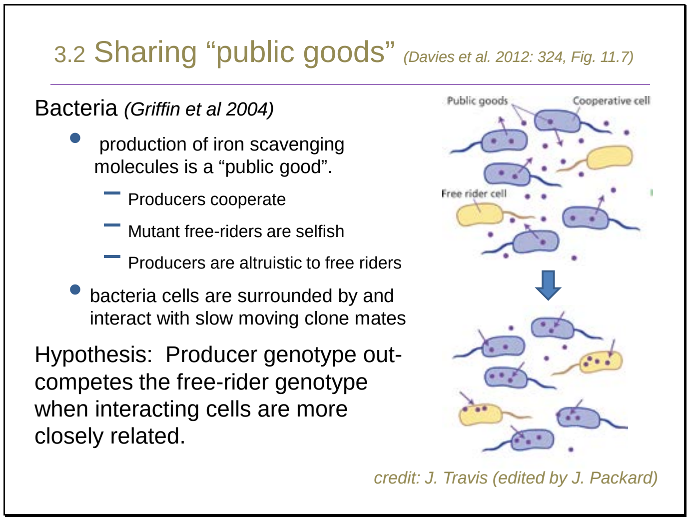
- H: “green beard effect”
  - If there is a genotype associated with kin discrimination
  - Then it would increase even if it had no apparent intrinsic benefit (e.g. green beard)
- Critique: unlikely to be common
  - Would one gene encode all three things (signal, recognition, and direction cooperation)?
  - Would a “cheater genotype” be likely to invade the gene pool?



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

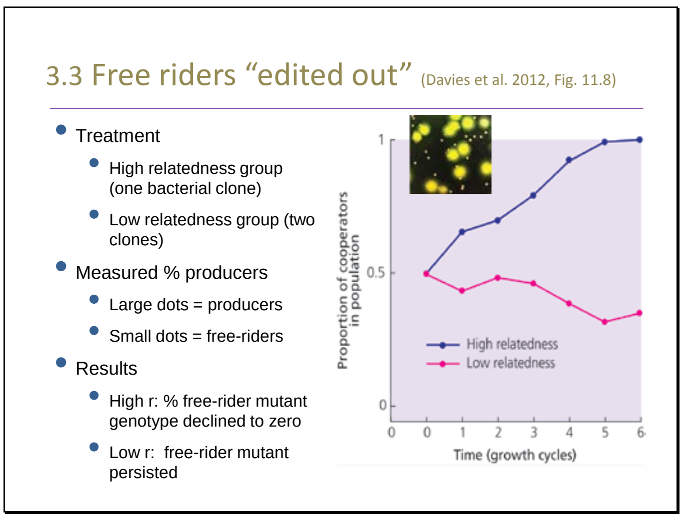
Think back to the fire ant example of kin discrimination. If individuals express “recognition alleles” phenotypically (such as having a “green beard”) and cooperate with others who express the same alleles (other individuals having a “green beard”)

Then it would be possible for individuals to join groups by displaying the “green beard,” but they do not perform any altruistic behaviors.

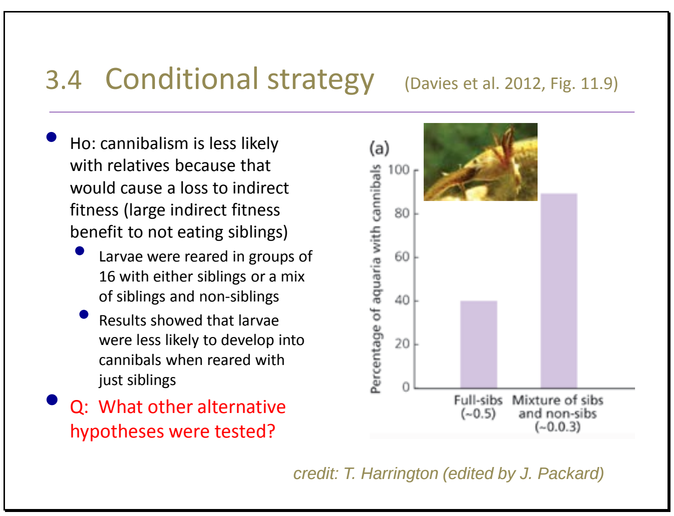


The science behind kin selection is moving more toward model systems like bacteria. Although the "green beard" effect has not been identified for bacteria, this example clarifies how the genetics behind kin interactions have been tested. These are the types of tests that would need to be done to test hypotheses about the "green beard" effect.

- What do the little arrows in the diagram illustrate?
- What is the change between the top and the bottom part of the diagram?
- What is meant by "free rider"? Public goods?



This study of bacteria is an example of how proportions of genotypes may shift in one gene pool compared to another over several generations. That is the type of information we need to test ultimate hypotheses. In this case we do not know the proximate mechanisms of kin discrimination.



Remember the study of the Arizona tiger salamander that was more likely to eat distant relatives than sibs?
To test kin selection in this example, we would need evidence that there were different genotypes, one that helped siblings and one that harmed them. What is the evidence that these morphs were a mixed (several genotypes) or conditional strategy (one genotype)?

Pfennig and Collins (1993) tested if salamander larvae development into cannibalistic morphs was influenced by interaction with relatives or non-relatives

Pfennig went further and used Hamilton's rule to test the kin selection hypothesis (but I do not agree with the way the data were interpretted, so am not going to use that example here)

Other hypotheses: disease,etc.

3.5 Hamilton's "Rule" (Davies et al. 2012, Fig. 11.9)

- Prediction: Altruistic genotypes will persist in a population if
  - B/C > 1/ r OR rB-C > 0
  - Benefits have to be much greater than costs, when "devalued" by the coefficient of relatedness
- Turkey Coalition (r = 0.42):
  - Coalition breeder=> 6.1 more offspring than solitary breeder
  - Solitary breeder => 0.9 offspring (equivalent to cost to coalition non-breeder)
  - Coalition non-breeder => 0 direct offspring
    - cost was 0.9 ; benefit was (0.42 x 6.1)- 0.9 = 1.7 inclusive fitness units
    - Since benefit > 0, the coalition non-breeder genotype would persist
- FP: "a gene can increase its transmission to the next generation by
  - Increasing its transmission to the next generation
  - Increasing the reproduction of other individuals carrying the gene"

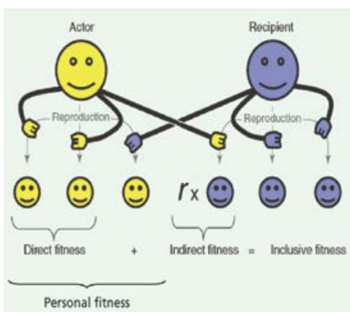
credit: T. Harrington (edited by J. Packard)

•To actually test Hamilton's "Rule", this is the evidence that would be needed. Note that this is not a rule, it is an hypothesis. It assumes that there are two different genotypes and the costs and benefits can be measured for each of these genotypes. In the case of the salamander, we know that there is only one genotype, that results in a conditional strategy, where individuals shift between "cannibal" and "non-cannibal" tactics.

•We need to define a few terms

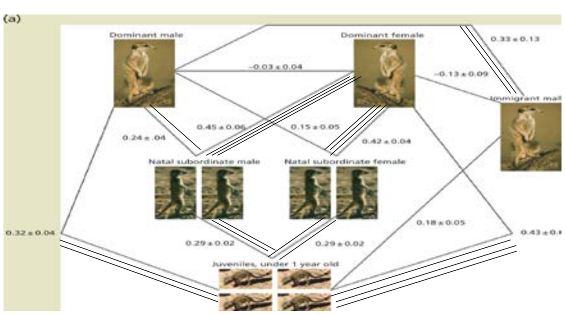
3.6 Inclusive fitness (Davies et al. 2012 Fig B11.4.1)

- Direct fitness plus indirect fitness
  - Actor's offspring
  - Recipient's offspring devalued by coefficient of relatedness (r)
- *Even though the actor's genotype is not replicated, it may be carried by relatives who do reproduce*



Lets define what we mean by inclusive fitness

3.7 Coefficient of relatedness (Davies et al. 2012, B11.3)



Lets define what we mean by the coefficient of relatedness, using this diagram for meerkats. Notice that technically r is defined relative the to probability that genes are shared by individuals taken at random from the whole population. Notice that the r between the two breeders is negative. What does that mean?

To fully understand how r is calculated, you would need to take an evolutionary genetics course. The take-home message is that kin selection is complex and we all need to be critical of sweeping statements that kin selection is an explanation of apparently altruistic behavior, when the assumptions have not been tested.

3.7 Poll- lets see if you understand

Kin selection is an explanation for apparently altruistic or spiteful behavior if you have:

- Evidence that benefits are greater than costs
- Costs and benefits are measured in direct fitness

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

b. Disagree. What is missing? Lets dialogue more about this using the elearning discussion tool

Summary

(Davies et al. 2012:331)

1. **Interactions of relatives:** mutually beneficial, selfish, altruistic, spiteful
2. **Kin discrimination (proximate):** coefficient of relatedness, kin recognition, care-giving directed preferentially to kin
3. **Kin selection (ultimate)**: inclusive fitness, Hamilton's rule, "green beard" effect, free riders

Take-home message. Kin discrimination predictions are easy to test. Kin selection is not! Be critical of glib explanations that altruism evolved through kin selection unless there is sufficient evidence to test the ultimate models. In your own writing, be very careful to distinguish between what is an hypothesis about kin selection and what is fact!

Be humble that we know just enough to "know what we do not know"! Take an evolutionary genetics course if you really want to understand the complex theory behind kin selection and group selection.