

## UNIT 11. ON SELFISHNESS AND ALTRUISM

**SOURCES** (for powerpoint format: <http://wfsc.tamu.edu/jpackard/behavior/wfsc622/powerpoints.zip>)

required: Chapter 11 in Krebs & Davies (1993:265-290)

remedial: "Living with Other Animals" in Halliday 1994; "Living Together" in the Trials of Life video series

supplement: Chapter 10 in Blumstein, D.T. and Fernandez-Juricic, E. "A Primer of Conservation Behavior"

### PARTS OF THIS LECTURE OUTLINE

1. Altruism Among Kin
2. Kin Selection
3. Hypothesis re: Non-Kin

*TIP1. Last unit was about co-evolution of "sneaker" and "caller" genotypes. This unit is about co-evolution of "selfish" and "altruistic" genotypes. The topic of altruism has received a lot of interest for two reasons. First, it has been viewed as the dividing line between humans (altruistic) and other animals (not-altruistic). Second, if the existence of true altruism can be clearly demonstrated, then the theory of natural selection would be disproved. So as you study this unit, keep in mind that much of the caring behavior that we observe may be "apparent altruism", meaning that it may appear to be an action that benefits the recipient more than the actor in the short term, but not in the long term. This unit also takes our understanding of "fitness" one step further. It distinguishes between "direct" and "indirect" fitness. This is where the aspect of kinship becomes important. "Indirect" fitness refers to the probability that a genotype for "caring" is not passed on directly through an individual's own offspring, rather by favoring the offspring of close relatives also likely to share the genotype for "caring". Notice that this implies the co-evolution of three behavioral traits: (1) "caring" (2) "distinguishing between kin & non-kin" and (3) directing caring behavior toward kin more than non-kin.*

### 1. ALTRUISM AMONG KIN

#### 1.1. Altruism- how could it evolve if natural selection favors individualism? (Krebs and Davies 1993:265)

1. Definition: action that increases the recipient's fitness at a cost to the actor's own fitness
2. Alternative hypotheses
  - a. H1: Kin selection (not really a cost to actor, because relatives share genes)
  - b. H2: Mutualism (both actor and recipient benefit)
  - c. H3: Manipulation (recipient "tricks" actor, an "arms race" in progress)
  - d. H4: Reciprocity (not really a cost to actor, because non-relatives reciprocate)

#### 1.2. Wife-sharing in the Tasmanian native hen (a flightless rail) (Krebs and Davies 1993:273 Table 11.2)

1. high OSR- more males than females=> breeding pairs and trios (2 males)
  - a. the actor tolerates another male; the recipient benefits by copulating with the female
  - b. cooperating males are either brothers or unrelated
2. trios produce more offspring than duos
3. game theory model (Krebs and Davies 1993:274 Box 11.2)
  - a. unrelated males: predicted payoffs were observed for 1st year, not later
  - b. related males: predicted payoffs were observed for lifetime fitness

#### 1.3. Alarm calls in ground squirrels and prairie dogs

1. Belding's ground squirrels (Krebs and Davies 1993:270 Fig. 11.1)
  - a. females with relatives nearby were more likely to call than females without
  - b. males disperse from relatives; less likely to call than females
2. black-tailed prairie dogs (Krebs and Davies 1993:272 Fig. 11.2)
  - a. males & females more likely to call with than without close relatives nearby
  - b. no difference between presence of offspring and less closely related kin

1.4. Take-home message: altruism between kin compared to non-kin

1. degree of relatedness between actor and recipient=> prediction of payoffs
2. e.g. Tasmanian native hen, ground squirrels, prairie dogs

Part 1	Study Questions for Chat & Quiz 11 "On Selfishness and Altruism"
1.1.1	What is the definition of "altruism" used by behavioral ecologists? (TIP: specify payoffs to both actor and recipient; explain the currency for payoffs)
1.1.2	What are four alternative hypotheses about the function of altruistic acts between kin? (TIP: KMMR)
1.2	For a bird species of your choice, how was the function of "apparently altruistic" interactions tested? (TIP: e.g. Tasmanian native hen)
1.3	For a mammal species of your choice, how was the function of "apparently altruistic" actions tested? (TIP: e.g. ground squirrels or prairie dogs)
1.4	For "apparently altruistic" interactions among kin, what is the predicted relation between relatedness and fitness payoffs? Why? (TIP: take home message)

2. KIN SELECTION

2.1 Hamilton's theory of kin selection (*Maynard-Smith 1964 cited in Krebs and Davies 1993:266*)

1. selection favoring traits that benefit survival of close relatives
2. inclusive fitness= direct fitness + indirect fitness (*Brown 1980 cited in Krebs and Davies 1993:266*)
  - a. direct fitness: offspring (personal reproduction)
  - b. indirect fitness: offspring of kin (devalued by coefficient of relatedness)
    - i. coefficient of relatedness (probability that a genotype is shared by a relative)
3. differs from the Prisoner's Dilemma Model of non-kin (*Krebs and Davies 1993:280 Table 11.4, Box 11.3*)

2.2. How do individuals distinguish between kin and non-kin?

1. H1: "green beard effect"- genotypes linked with altruistic genotype (unlikely)
2. H2: "treat anyone in my home as kin" (only kin are likely to be home)
3. H3: imprinting- follow the first moving object you see (likely to be mom)

2.3. Do individuals direct different actions to kin and non-kin?

1. cross-fostering experiment in ground squirrels (*Krebs and Davies 1993:276 Fig. 11.3*)
  - a. split litters=>
    - i. siblings reared together (S:RT) and reared apart (S:RA)
    - ii. non-siblings reared together (NS:RT) and reared apart (NS:RA)
2. fights directed more to unfamiliar individuals (siblings or non-siblings)
  - a. field observations: full sisters fight less & aid more in chases than half sisters

2.4. Take-home message- Kin Selection

1. models predict that altruistic genotypes may persist if they benefit close kin
2. test requires (a) recognition of kin AND (b) acting differently toward kin than non-kin

Part 2	Study Questions for Chat & Quiz 11 "On Selfishness and Altruism"
2.1.1	What is Hamilton's theory of kin selection? (TIP: you may use Maynard-Smith's rewording of the theory)
2.1.2	Define the following terms: "inclusive fitness", "coefficient of relatedness"? (TIP: explain direct/indirect fitness)
2.2	What are three alternative hypotheses about how individuals distinguish between kin and non-kin? (TIP: GHI)
2.3	What is the evidence that individuals differentiate between kin and non-kin in the way they direct their behavior? (TIP: e.g. cross-fostering in ground squirrels)
2.4	If you were doing a study on apparently altruistic behavior among kin, what data would you collect? (TIP: take-home message re. kin selection)

### 3. HYPOTHESES RE. NON-KIN (MMR)

#### 3.1 H1: Mutualism (*Krebs and Davies 1993:278-279 Table 11.3*)

1. African lions: male coalitions take over breeding female groups
2. breeding male duos and trios were likely to be unrelated (larger groups were brothers)
3. average reproductive success per male increases with coalition size
  - a. larger coalitions were able to defend a female group for more years
  - b. dominant males sired more cubs than subordinate males
  - c. subordinates sired more cubs than if they stayed out of a coalition

*TIP2. Notice that this is where the time scale becomes important. In the short-term, individual males may appear to be altruistic because they let unrelated males breed during the estrus of one lioness. However, over the long-term, there is no overall fitness cost to the actor if the relative payoffs are calculated in terms of lifetime reproductive success.*

#### 3.2. H2: Manipulation (*Krebs and Davies 1993:279*)

1. altruistic actor: female starlings raise nestlings that are not their own
  - a. benefit to unrelated female (recipient) who laid egg in the actor's nest
  - b. cost to altruistic female who raises 1 less offspring than otherwise
  - c. dump-nesting recipient removes 1 egg from the altruistic female's nest
2. recipient "tricks" the altruist=> likely to be selection for a counter-strategy

*TIP3. Notice that this is a "backwards" argument. The altruist is the female that receives the egg in her nest. It is not her action that sets up the situation, it is the action of the beneficiary, the parasitic female who lays the egg. This example is confusing for many students, because we can look at it from two perspectives. From the perspective of the parasitic female, the action of laying an egg in another female's nest is "selfish". From the perspective of the recipient of the egg, her action is "altruistic" because she is caring for young that is not her own. However, over a longer time frame of many generations, behavioral ecologists would predict that natural selection would favor genotypes that discriminate against the "altruistic" genotype rearing the unrelated chick. In other words, this is a good example of an academic mind game. It reminds us that an "Arms Race" never really ends, it may just slow down during periods of relatively little change in the environment.*

#### 3.3. H3: Reciprocity

1. spawning in black hamlet fish (simultaneous hermaphrodite) (*Krebs and Davies 1993:285*)
  - a. "tit for tat"- donor leaves if partner does not reciprocate with eggs
2. regurgitated blood meals between unrelated vampire bats (*Krebs and Davies 1993:286 Fig. 11.4*)
  - a. more likely to feed familiar bats, more likely to reciprocate, at no cost
3. grooming alliances in unrelated vervet monkeys (*Krebs and Davies 1993:287 Fig. 11.5*)
  - a. increased the probability that they reciprocated to solicitation for aid in fights
4. unrelated male coalitions in consortships: olive baboons (*Krebs and Davies 1993:288 Fig. 11.6*)
  - a. one male fights rivals while the other male copulates, roles are reversed with another female

#### 3.4 Take-home message: alternative hypotheses re. altruism between non-kin

1. mutualism, manipulation, reciprocity (MMR)
2. e.g. African lions; starlings; black hamlet fish, vampires, vervets, olive baboons

Part 3	Study Questions for Chat & Quiz 11 "On Selfishness and Altruism"
3.1	For altruistic behavior among non-kin, how was the Mutualism Hypothesis tested? (TIP: e.g. lions)
3.2	How was the Manipulation Hypothesis tested for a study of altruistic behavior between non-kin (within one species)? (TIP: e.g. dump-nesting in starlings)
3.3	was the Reciprocity Hypothesis tested for a study of altruism between non-kin? (TIP: e.g. vampire bats)
3.4	What are three alternative hypotheses about the function of apparently altruistic behavior among non-kin? (TIP: MMR)

**SUMMARY**

- 1. Altruism between kin compared to non-kin**
  - a. degree of relatedness between actor and recipient influences the prediction of payoffs
  - b. e.g. Tasmanian native hen, ground squirrels, prairie dogs
  
- 2. Kin Selection models predict that altruistic genotypes may persist if they benefit close kin**
  - a. test requires
    - i. recognition of kin
    - ii. acting differently toward kin than non-kin
  
- 3. Altruism between non-kin: alternative hypotheses**
  - a. mutualism, manipulation, reciprocity (MMR)
  - b. e.g. African lions; starlings; black hamlet fish, vampires, vervet monkeys, olive baboons

Summary	Study Questions for Chat & Quiz 11 "On Selfishness and Altruism"
4.1	What are three take-home messages about this unit on apparently altruistic behavior between kin and non-kin? (TIP: summary)
4.2	Why would apparently altruistic behavior persist in a population if it resulted in lower fitness of the actor? (TIP: summary)

*TIP4. From a practitioner's perspective, this unit may appear to be more about academic mind-games than it is about practical knowledge that can be used in management decisions. However, this unit also sets an important foundation for the next unit. Basically, it reminds us to keep an open mind. Sometimes animals do behave in ways that are not entirely selfish. On the other hand, we cannot expect individuals to make sacrifices for the "good of the species". Each species and each population needs to be examined carefully, in its own environment and circumstances. In the next unit, we will learn more about helping behavior. It is a behavioral adaptation that differs from altruism, because it is an extension of parental care, directed toward individuals that are not the direct offspring of the actor. In other words, in the present unit, we "lay to rest" the arguments about altruism between non-kin, setting the stage in the next unit to look in more detail at the behavioral adaptations of "caring for kin".*