

## **The evolution of social behavior: Altruism and kin selection**

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- It was not difficult to understand how selection can affect mating and parenting behavior, and behaviors directly related those
  - because these behaviors obviously and directly affect reproductive success
- but primates also interact with each other in many other ways that are not directly related to sex and offspring
  - grooming
  - alliances in conflicts with others
  - warning or defending others from predators
  - adults insisting on inspecting others' infants
  - adults caring for others' infants
  - etc.
- these behaviors do not have an obvious, direct connection to reproductive success
  - so it would seem that they would be hard to explain in evolutionary terms
- human intelligence probably evolved from simpler, but still complicated, behaviors like these
  - so understanding how these behaviors evolved is crucial to understanding our own origins
- In fact, evolutionary theory *can* help us understand how many of these social behaviors could be favored by natural selection
- First, let's be more specific about what kind of behavior we mean
  - we can categorize social interactions between two individuals according to whether they produce a *benefit* or a *cost* for the reproductive success of each of the two individuals involved
  - we consider one individual to be the “actor”; the other is the “recipient” of the behavior
    - “selfish” behavior: benefits actor, costs recipient (or is neutral)
    - “mutualistic” behavior: benefits both actor and recipient (“win-win”)
    - “spiteful” behavior: costs both the actor and the recipient
    - “altruistic” behavior: costs the actor, but benefits the recipient
  - naturally, these terms are just shorthand
    - they don't necessarily imply any understanding or emotion on the part of the animals
    - as we saw before, it is very difficult to really measure reproductive success without a large, expensive, long-term project in which we count the number of surviving offspring over several years
      - so primatologists usually substitute shorter-term costs or benefits like exposure to predators or increased access to food
      - assuming that these will generally have the expected positive or negative effects on reproductive success, which is what really matters
  - Not surprisingly, “selfish” behavior is common in competition for food, mates, etc.
  - “mutualistic” behavior also occurs, but is harder to observe than you might think
    - two individuals grooming each other at the same time

- two individuals hunting together
- Also not surprisingly, “spiteful” behavior is rare, since it reduces the reproductive success the actor
- what *is* surprising is that primates engage in a lot of “altruistic” behavior
  - one individual grooms another
    - spends time that it could be using to find food, mates, rest, etc.
    - while the other benefits from having its fur cleaned, parasites removed, wounds cleaned, etc.
  - an individual gives a warning call when it sees a predator
    - calling attention to itself and increasing its risk of predation
    - while benefiting the others by improving their chances to escape
  - an individual backs up another in a conflict
  - an individual shares food with another
  - lots of human behavior is altruistic in this technical sense:
    - sharing food
    - helping others with their work
    - caring for the sick, injured, or old
    - doing anything that involves some degree of sacrifice for the good of another individual or the group
  - it seems obvious that selection would not favor a tendency to do something that would reduce the actor's reproductive success and increase another's
    - say some individuals sacrifice their lives to protect others from predators
    - you would think that their “altruistic” genes would quickly be eliminated from the population, as they die off and others, who don't sacrifice themselves, reproduce
  - even if a behavior helps the group as a whole, ordinary selection would not favor it
    - say some individuals have an allele that makes them prone to give a warning calls when they see a predator
      - it is not unrealistic to suggest that a tendency to give warning calls could be influenced by one (or several) alleles
      - for example, the “warning call” allele might cause a higher production of adrenaline, making the individuals who have it more jumpy and prone to make noises
      - and you know that dogs can be bred for traits like barking more or less; some breeds are yappy and others rarely bark
    - if one individual gives a warning call, all the others in the group benefit, regardless of whether or not they carry the warning-call allele(s)
    - but the one who gives the warning call is more likely to get eaten
    - so there is no direct benefit to having the allele, and there is a cost
    - so selection should weed out the warning-call allele
- but there *is* a situation in which selection would favor “altruistic” behavior
  - called **kin selection**: selection in which a trait becomes more (or less) common because it affects the reproductive success of *relatives* of the actor more than non-relatives
    - because the relatives have some of the same alleles as the actor

- so if a behavior like giving a warning call when a predator is sighted improves the reproductive success of many of the caller's relatives, the total number of “calling” alleles that get into the next generation might be higher, even if the caller himself gets eaten
- as we know from Mendelian genetics, an individual shares some of its alleles with its relatives
  - the closer the relative, the more alleles they have in common
  - for example, a child shares one half of its alleles with each parent
    - one of each pair of alleles came from each parent, so one half of the alleles in the offspring are from the mother, and one half are from the father
  - grandparents share one quarter of their alleles with grandchildren
  - siblings (brothers and sisters) also share one half of their alleles with each other
    - each sibling got half of the mother’s alleles, but not necessarily the same ones
      - in fact, for any allele I got from my mother, there is only a 50% chance that my sister also got it from my mother
      - so I share only 25% of my mother’s alleles with my sister
    - but each sibling also shares half of the father’s alleles
      - so I share 25% of my father’s alleles with my sister
    - in total, I share 50% of my alleles with my sister
  - and so on...we could figure out the shared alleles for any relative
    - half of an individual’s alleles are passed on along each link in the family tree, so each link separating two individuals in a family tree reduces the fraction of shared alleles by half
      - (remembering that full siblings are related by two paths of links, because they have both parents in common)
- the fraction of alleles that two individuals share is their “coefficient of relatedness”
  - the higher the coefficient of relatedness, the more alleles in common, and the closer the relationship
  - parent-offspring: 0.5
  - sibling-sibling: 0.5
  - half-siblings: 0.25
  - grandparent-grandchild: 0.25
  - sibling's offspring (uncle-nephew, etc.): 0.25
  - unrelated: 0.0
    - even though unrelated individuals may happen to share some alleles, this is not by descent
    - on average, any pair of unrelated individuals shares no more alleles than they do with any other unrelated individuals
- The key to kin selection:
  - What affects evolution is how many copies of an individual's alleles get into the next generation
  - it does not matter if they get into the next generation through the individual's own offspring or through the offspring of relatives

- the only difference is that relatives have only some of an individual's alleles, so it will take more of their offspring to get the same number of copies of the individual's alleles into the next generation
- Example of kin selection
  - Your own offspring carry 50% of your alleles
  - Your sibling's offspring carry 25% of your alleles
  - So if you do something that increases your sibling's reproductive success by two offspring, the effect is exactly the same as if you had one more child yourself
  - If your action does not reduce your own reproductive success by one, then the tendency to do that action will become more common
  - as far as evolution is concerned, two children of your sibling have as much effect on the next generation as one child of your own
  - the same comparisons can be made with all other relatives
    - two of your grandchildren carry as many of your alleles as one of your own children, and so on
    - two nephews are equivalent to one child
    - four great-grandchildren are equivalent to one child, etc.
- what we are doing here is correcting an oversimplification in our model of evolution
  - before, we said that natural selection favored traits that increased an individual's reproductive success
    - where reproductive success was measured by how many offspring that individual contributed to the next generation
  - now, with our knowledge of genetics, we can revise that
  - New version: Natural selection favors traits that increase **inclusive fitness**
    - **inclusive fitness**: the total number of copies of an individual's alleles that are passed on to the next generation
      - both directly, through offspring
      - and indirectly, through the offspring of relatives
    - natural selection does NOT simply favor traits that maximize reproductive success
    - instead, natural selection favors traits that increase *inclusive fitness*
- so now, say a bunch of baboon siblings are out foraging, and one sees leopard
  - the one who sees the leopard gives a warning call
  - the caller incurs a cost, since it has drawn the leopard's attention and is slightly more likely to get eaten
  - but the siblings get the benefit of being warned before they saw the leopard, helping them escape and reducing the chance of the leopard getting close enough to kill several of them.
  - half of the siblings have the alleles that encourage giving warning calls, just because they are siblings of the caller
  - if the total benefit to the siblings is large enough, it can outweigh the cost to the caller
    - the net effect is that more of the calling alleles get into the next generation through the siblings than were lost by the possible demise of the caller
    - that is, by considering inclusive fitness, we see that selection can actually favor traits that are fatal!
- we can specify this precisely using Hamilton's rule

- which simply says that an “altruistic” behavior will be favored by selection if the cost is less than the total benefit discounted by the coefficient of relatedness
- $rb > c$
- where  $r$  = average coefficient of relatedness between actor and recipients
- $b$  = total benefit to all recipients (number of offspring gained as a result)
- $c$  = cost to the actor (number of offspring lost as a result)
- take the case of you and your sister ( $r = 0.5$ )
  - you save her from drowning, but as a result, you die from pneumonia
  - you would have had one more child
  - she goes on to have three more children
  - $0.5$  relatedness  $\times$  3 children gained  $>$  1 child lost
  - the alleles that lead you to be altruistic towards your sister are increased in frequency in the next generation
- take the case of your dumb neighbor
  - he saves the unrelated girl down the block from drowning, but he dies of pneumonia
  - he would have had one more child; she goes on to have three children
  - $0.0$  relatedness  $\times$  3 children is NOT  $>$  1 child
  - the alleles that lead him to be altruistic towards non-kin are *reduced* in frequency in the next generation
- that is, altruistic behavior is only favored when it benefits sufficiently close kin
  - but that will often be true for social animals like primates
  - because primate females usually stay in the group they are born into
  - so most of the members of the group are relatives
    - related females
    - their offspring, which are also obviously related
    - and some males, many of whom are related to some of the offspring
  - so any altruistic act is automatically likely to help some relatives
    - just because most of the individuals nearby are usually relatives
- The closer the relative, the more costly the acts of altruism that may be favored
  - because the more alleles the relative shares with the actor
  - so our feelings of closeness to siblings, for example, may have a biological basis
    - there are clear evolutionary reasons for our willingness to help a sibling more than a random person on the street
  - nepotism (favoring relatives in business, politics, etc.) is not just corruption; it probably has deep evolutionary roots
- of course, Hamilton's rule also shows when altruism will *not* be favored
  - even between the closest relatives (sibling-sibling, parent-offspring,  $r=0.5$ ), the benefit to the recipient has to be at least *twice* the cost to the actor
  - so consider what happens when siblings compete directly, as for food, attention from the mother, etc.
    - what one sibling would personally gain by another altruistically giving way is about the same as what the altruist would give up

- yet its offspring only carry half as many of the actor's alleles as the actor's own offspring will
- so that sort of balanced altruism would not be favored; siblings compete with each other intensely
- There is good evidence that kin selection really does occur among primates (and other animals)
  - For kin selection to work well, primates would have to be able to recognize their relatives
    - so that they would correctly direct altruistic acts towards closer relatives, and not lose inclusive fitness by benefiting distant relatives or non-relatives
    - field observations suggest that many primates do recognize their relatives
    - some animals recognize their relatives without learning, perhaps using chemical clues (smell)
    - but primates apparently have to *learn* who their relatives are
      - a primate mother will accept a stranger's infant as her own if it is swapped early enough
        - that is, she has to learn to recognize the infant; she does not recognize it by a smell similar to her own, or any other inborn trait
      - primate mothers study their infants carefully
      - other related individuals do too
      - juveniles pay a lot of attention to their mothers' new infants
      - the infants get to know the mother and their siblings, who are around the most
      - notice that all of this learning is in the context of the infant with its mother
      - individuals who have the same father but different mothers will never learn that they are related!
  - if kin selection is the correct explanation for altruistic behavior, then most altruism should occur between close kin
    - lots of evidence indicates that it does
    - food sharing is altruistic
      - it costs the giver some of the food
      - and benefits the recipient
      - and the vast bulk of the incidents of food sharing is between kin related through the mother
        - primarily mothers and offspring
    - grooming is altruistic
      - it is more common among kin than non-kin
      - especially mothers and offspring
    - coalitions are altruistic
      - one individual backing up another in a conflict
      - may be dangerous for the one providing support
      - most often formed by close kin
      - especially common between mothers and offspring
      - but also among siblings, half-siblings, grandparents-grandchildren
  - in many species with female dominance hierarchies, the mother supports her female offspring in dominance disputes

- this generally gives the female offspring the position just below the mother in the dominance hierarchy
- this makes the female dominance hierarchies extremely stable, generation after generation
- all the descendents of one mother will rank above all the descendents of a lower-ranked mother
- this is altruism on the mother's part, since it carries some risks
- and it generally benefits only her own offspring, so it makes good sense in terms of kin selection
- all of parental investment is really just a special case of kin selection, where the altruist is the parent and the recipient is the offspring
- male cooperation in red howler monkey
  - in these small multi-female, multi-male groups, only the highest-ranking male fathers all the offspring
  - yet all the resident males work together to drive off cooperating groups of bachelor males
    - this can incur severe costs to the defending males, including those who are not mating themselves
  - why help drive off bachelor males, then?
    - apparently because the cooperating males are often related
    - keeping away the unrelated bachelor males increases their inclusive fitness, through the offspring of a related male
    - evidence
      - coalitions of related males last almost four times as long as coalitions of unrelated males
- There is another, completely different mechanism that might select for altruistic behavior: reciprocal altruism
  - **Reciprocal altruism:** altruistic behavior that is selected for because the altruist is consistently repaid more than the cost of the action
    - this is easier than it sounds, since the cost of performing a service like grooming is low; probably less than the benefit of receiving it
    - so if a recipient of grooming reciprocates with a grooming session for the actor, that more than compensates the altruistic actor for the cost of giving the grooming in the first place
    - under the circumstances of dependable repayment, natural selection should favor the tendency to be altruistic, because it benefits the actor directly just a little while later
    - in a sense, the behavior is only “altruistic” temporarily, until it is repaid
  - This process of reciprocal altruism could favor altruistic behavior if:
    - individuals interact frequently
      - frequent interaction is necessary in order for there to be opportunities for altruistic actions to be repaid
    - individuals can keep track of who they have helped and who has helped them
      - the ability to keep track of who you helped and who helps you is necessary to be able to carry out the third, key part:

- individuals only help those who help them
  - those that help others and reciprocate will get more help than those that don't
  - that is, those that are altruistic do benefit more than those who are not, and leave more offspring
  - so if some individuals start showing the altruistic tendency and others repay it, altruism will be selected for
- these conditions seem to be met by many primates
  - they do interact frequently
  - can they keep track of “debts” and who does and does not pay back? maybe--
    - we know that they can recognize individual relatives
    - and that they regularly solve complex social problems
      - like dominance hierarchy relations
      - coalition formation
  - and field data suggest that some primates do tend to help those that have helped them
    - male bonnet macaques tend to support those that have supported them in conflicts
      - also those that groomed them most often
    - vervet monkeys respond most strongly to vocal calls for support from individuals who have recently groomed them
      - shown by Dorothy Cheney and Robert Seyfarth's tape recorder studies
  - male chimps
    - tend to share meat primarily with other males who
      - have shared meat with them
      - and who support them in conflicts with others
    - male chimps who hunt together also
      - tend to groom each other more
      - support each other in conflicts
      - and go on “border patrols” together
    - but these males tend NOT to be maternal relatives
    - so their cooperation is probably based on reciprocity, not kin selection
- Both kin selection and selection for reciprocal altruism probably do occur
  - both appear to work to increase the tendency to do “altruistic” acts
  - which are the basis of a lot of complex behavior
  - especially human, cultural behavior
  - so this gives us an idea of how the basic behavioral tendencies that make us human may have originally been selected for.
- next time, we will look at how all this complex behavior ties into the evolution of what really sets primates, and especially us, apart from other animals: intelligence.
-