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 or coalitions in conflicts with others; warning or defending others from predators; adults insisting on inspecting others’ infants; adults caring for others’ infants, etc.

complex behaviors like these were presumably the starting point for the evolution of our own complex social behavior and intelligence.

there are two (at least) ways that evolutionary theory can explain this sort of complex social behavior…

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, at least.

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.

two individuals grooming each other at the same time

several individuals hunting together

a few lower-ranking males jointly attacking the dominant male in a group.

Also not surprisingly, “spiteful” behavior is rare, since it reduces the reproductive success of the actor.
what is surprising is that primates engage in a lot of “altruistic” behavior
one individual grooms another (allogrooming, vs. self grooming, which is also called autogrooming)
the actor spends time that it could be using to find food, mates, rest, etc.
while the recipient 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 benefits one or more other individuals, but costs the one doing it

The tendency to do specific behaviors that are altruistic could be partially genetic
for example, a tendency to give warning calls could be influenced by one (or several) alleles
different breeds of dogs are yappy or quiet
this is genetic: due to breeding for certain characteristics
it makes them more or less likely to give alarm calls, which can be an altruistic behavior
a “warning call” allele might cause a higher production of adrenaline, making the individuals who have it more jumpy and prone to make noises

But altruistic behaviors reduce reproductive success. Why doesn’t natural selection weed out the alleles that encourage altruism?
say some individuals have an allele that makes them prone to give a warning calls when they see a predator
if one individual gives a warning call, all the others in the group benefit, 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 due to having shared ancestors 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
half-siblings: 0.25
full siblings: 0.5
grandparent-grandchild: 0.25
sibling’s offspring (uncle-nephew, etc.): 0.25
unrelated: 0.0
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 add as many of your alleles to 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 a 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 to the individual with the trait!

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.
- Natural selection will favor a behavior if $rb > c$.
- 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 x 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 x 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
- but recent evidence goes even further: many primates do recognize their close kin and tend to hang out with them more than with more distant kin in the same group
- they use both contextual cues
  - learning to recognize infants and siblings because they tend to be together near their mother
  - preferring to hang out with others of a similar age
    - age-mates were conceived around the same time
    - so they are likely to have the same father: the male that was most dominant at that time
    - so they are kin, and share alleles
  - and using phenotypic matching
    - clues to relatedness based on smell or other physical similarities
- so the conditions for kin selection to favor altruism must be fairly common

What about humans?
- We generally feel most connected to our closest relatives
  - Parents, children, siblings
  - This makes good evolutionary sense!
    - Our emotions have apparently evolved such that we tend to direct the most altruism towards our closest relatives
    - Those who share the most of our alleles
    - Whose reproductive success adds the most to our own
    - there is a lear evolutionary reason 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.
– if an altruistic sibling gives up \(X\) amount of maternal care, the recipient sibling gains that same \(X\) amount
– but the recipient sibling only carries half of the altruist’s alleles
– the cost to the actor is twice the benefit to the recipient \(x\) their relatedness
– so that sort of altruism would not be favored
– siblings compete with each other intensely for food, attention, etc.
– except where the benefit to the recipient is much greater than the cost

– 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, using phenotypic matching, perhaps chemical clues like smell
– but many primates 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
– this takes time and effort, so it must serve a function
– presumably to direct altruistic behavior towards the closest relatives
– most observed altruistic behavior does happen between close relatives
– 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
epecially 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
as in figure 7.14 in the textbook with a juvenile and an older female baboon facing off against another female
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
since it benefits 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 invading 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 benefit more than those who are not, and leave more offspring
– so if some individuals tend to be altruistic and others repay it, the 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 playback 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.