19. Societal Evolution

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Altruism, Cooperation, the Prisoner’s dilemma and other social games

Reciprocal Altruism and the Prisoner's Dilemma
Tit for Tat and the Iterated Prisoner's Dilemma

Cases of Tit for Tat in Nature
  Neighbor-Stranger Recognition and Tit for Tat
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The Evolution of Cooperation

True Altruism, Cooperation, and the Prisoner’s Dilemma

The dear enemy relations discussed in Chapter 8 suggest that territorial competition need not lead to escalated conflict. The evolution of cooperation in unrelated individuals, such as neighbors involved in a dear enemy truce, begs an explanation consistent with evolutionary theory. There must be some fitness advantage derived from cooperation among unrelated individuals.

In Chapter 4, 11, and 19, we have already dealt with many of the issues underlying the evolution of cooperation among closely related kin. In the case of social hymenoptera, kin selection is accentuated by the generally higher degree of relatedness among sisters compared to other groups. The kind of sacrifices individuals are willing to make in the case of kin can be understood in terms of Hamilton's equation for inclusive fitness (see Chapter 4). An individual may opt to aid kin because such an act would enhance that individual’s inclusive fitness: their own genes and the total number of genes shared with the kin.

True altruism is defined as behavior, which is detrimental to an individual's fitness (cost), but enhances another individual’s fitness (benefit), and the two individuals do not share a genetic relationship. In human relationships, some individuals appear to aid non-related individuals, and in some cases it is clear that there can be no relationship between the giver and recipient of the altruist act. Mother Teresa’s acts of kindness for the poor of India appears to be exactly such a noble gesture; a truly altruistic act (especially in light of a nun’s vow of chastity). Many contend that it is exactly these kinds of explanations that may actually reside outside the sphere of biological explanations. Such altruism is difficult to reconcile in terms of evolutionary models.

Cooperation is a behavior that occurs between two unrelated individuals that has a net mutually beneficial effect on the long-term fitness of both individuals, but the act may entail fitness costs in the short-term.
Robert Trivers (1971) was one of the first evolutionary theorists to consider the case of true altruism and the conditions required for the spread of altruistic genes. He noted that if an altruist distributed their acts randomly in the population, the altruist gene would ultimately disappear as cheaters could easily take advantage of the altruist, but not give back in return. The altruist must receive some benefit from its actions. Alternatively, social systems must be constructed in ways that limit the spread of cheating (e.g., social networks limit its spread).

How do altruistic acts arise? Trivers realized that altruistic genes might spread if altruist did not distribute his or her good deeds randomly, but rather distributed them to other individuals that showed evidence of reciprocity. This is referred to as reciprocal altruism.

Triver's insights did not really catch on until Axelrod and Hamilton (1981) developed game theory models describing the evolution of altruism. As was the case with Maynard Smith’s formulation of Evolutionary games (1982) in which models and principles were extensively borrowed from economists (e.g., Nash equilibrium, Chapter 7), models on cooperation were likewise borrowed from economics (Selten, etc.). We will explore the issue of reciprocal altruism with their simple models of cooperation -- the prisoner’s dilemma and the iterated or repeating prisoner’s dilemma (Axelrod and Hamilton 1981).

Consider two prisoners that are caught with stolen goods (see Side Box 8.2). The district attorney (DA) places them in separate rooms. She offers each the same deal: snitch on your partner and you’ll be set free. Your partner who you have implicated in the crime will receive a stiffer penalty. However, if both prisoners snitch, neither will gain freedom because they implicated each other in the crime. [Remember, when the DA on Law and Order interrogates two criminals, these interrogations are conducted in separate rooms. If the prisoners opt to cooperate with each other and not snitch, the DA will have very little evidence against the two and the punishment will only be light. The paradox of the prisoner’s dilemma arises because the Evolutionary Stable Strategy should be to defect if only a single round of play takes place. Player B’s strategy is independent of player’s A’s strategy (they are in separate rooms), and thus the highest payoff for player B, freedom, is to defect. The same is true for player A. The temptation to defect leads to mutual defection. Mutual defection is a much lower payoff than mutual cooperation, but being locked in separate rooms the Player’s cannot talk it over and come to the cooperative arrangement. The possibility of being left with the sucker’s payoff (being snitched on while your partner chooses to defect to the DA, and thus be set free), is motivation enough to defect. You are tempted to snitch on your partner-in-crime before he/she snitches on you. You both end up defecting on the partner-in-crime and the DA has enough evidence to serve up a stiff punishment.

**Side Box 8.2. The Prisoner's Dilemma**

Axelrod and Hamilton (1981) investigated algorithms for behavior in a game of cooperation that illustrates conditions necessary for the evolution of cooperation. Consider two prisoners in a jail who were caught with stolen property. The district attorney interviews the prisoner's separately. There are four possible outcomes from the process of interrogation:

1. The prisoners know that if they both keep quiet, there is not enough evidence to be convicted of theft. They just get 1 year for possession of stolen goods.
2. If both prisoners confess to theft they get 5 years in jail.
3. If one rats on the other who keeps quiet, then the stool pigeon goes free (0 years), and
4. the other prisoner gets 10 years, one extra year for not helping the police in their investigation.

What should they do? A payoff matrix describes the consequences of confessing or keeping quiet for player A (because the same matrix
applies for B the game is symmetric):

<table>
<thead>
<tr>
<th>Player A</th>
<th>Cooperation</th>
<th>Defection</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cooperation</td>
<td>-1</td>
<td>-10</td>
</tr>
<tr>
<td>Defect</td>
<td>0</td>
<td>-5</td>
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</table>

Table 19.1

Let us consider the value derived from all four possible plays and their payoffs (D|C is read as follows “player A defects given that his partner, player B, cooperates”):

DIC > ClC > DID > CID

DIC is referred to as the temptation to defect.

ClC is referred to as mutual cooperation

DID is referred to as the punishment for mutual defection.

CID is referred to as the sucker's payoff.

Player A should defect because DIC is the best payoff. However, player B should do the same because the game is symmetric and neither knows what the other will do. When both defect they get a worse payoff than if both had cooperated. In the long run, that is if the players were to consider the future consequences of their behavior, then it pays to cooperate (ClC) because it provides the second highest payoff. The best strategy for both players is to cooperate as the average payoff for each is (-1-1)/2 = -1. However, the temptation for freedom (payoff = 0) is great enough that a greedy prisoner might opt for it and the average payoff for both is (0-10)/2 = -5. Because no one wants to get a sucker’s payoff, it is likely that both would opt for defection where the average payoff is (-5-5)/2 = -5, even though cooperation would give a better payoff. Therein lies the dilemma. The students’ dilemma applies given payoffs with a reward structure as follows:

Temptation > Cooperation > Mutual defection > Sucker's payoff

The students are locked in the prisoner’s dilemma.

**Tit for Tat and the Iterated Prisoner's Dilemma (IPD)**

Axelrod and Hamilton (1981) challenged behavioral ecologists from around the world to come up with the strategy that would perform best when playing the prisoner’s dilemma. Scientists submitted their algorithms to Axelrod and he set the bits in motion and came up with a winner -- the iterated Tit-for-tat, or TFT for short beat all the other algorithms. This is an evolutionary tournament of sorts. TFT chooses to
cooperate on its first opening move, and then on its next moves, it plays the identical move that the opponent played on their last move. In a population of reciprocal altruists, TFT ends up with high average fitness (e.g., cooperation -- the best average outcome for two opponents). Likewise in a population of defectors, TFT ends up defecting on the second move and minimizing the sucker’s payoff.

The original paradox of the single play prisoner’s dilemma arises because the Evolutionary Stable Strategy should be to defect if only a one round is played (see Side Box 8.2). Let’s consider the iterated “student’s dilemma” (see Side Box 8.2), but consider the choices when the students know one another (of course they know each other because they cheated at the outset). The two students will ultimately take courses with one another throughout their tenure as students. If the professor engages the two in the student’s dilemma, they will probably cooperate because of the possibility of future reciprocity that is inflicted on a defector (not to mention the stigma of being a stool pigeon). The two might get caught and lose grades for the final, but the two still have a good chance of passing the course (particularly if they have a high grade going into the final from all their cheating). If their partner cooperates, they should also cooperate, provided they keep up this strategy throughout the duration of their studies. If their partner defects then they will defect on the next test and cooperative association will dissolve away. The iterated TFT holds the two students in a cooperative alliance.

There are in fact three play movements that make Tit-for-Tat the unbeatable strategy, or the ESS.

- The TFT is nice when both players cooperate on the first move of the game.
- However, TFT can also retaliate. When one partner defects TFT will also defect.
- Finally, TFT is also forgiving in that a past defector that has chosen to cooperate will receive cooperative behavior in return.

In the long run, it pays to cooperate, providing that the individual recognition and discrimination exists to exclude the cheaters.

The evolution of cooperation via a TFT strategy as a solution to the iterated Prisoner’s Dilemma makes it possible for unrelated individuals to participate in a kind of cooperative interaction. Cooperation forms the kernel for many kinds of social interactions in this Chapter on Social Evolution. Behaviors that underlie such reciprocal altruism could arise and spread in a population, if and only if, altruists can distinguish cheaters. Indeed, in human societies this particular formalism is bundled up in many human transactions. Credit card companies and the credit card holder have tit-for-tat relations. Draw up a payoff matrix for the following game. If a credit card company does not loan money it does not gain interest from loaning. The temptation to cheat is for the credit card holder to ring up the card to the max and declare bankruptcy, but keep their toys. Although a delinquent debtor does get a short-term payoff, the bad credit rating makes it impossible to get money in the future. Thus, the debtor pays off debts and the credit card company takes in interest. The debtor gains the buying power for more goods (e.g., a house) that they might not have otherwise. The can get more loans and the game is iterated anew.

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**Tit for Tat in the Nature**

Here, we will explore evidence for TFT behaviors in Nature. The evolution of tit for tat is contingent on a number of other behaviors such as individual recognition of partner in the cooperation. Direct evidence of the payoffs may not be possible in many situations, but evidence of TFT behaviors might suggest that some version of the IPD is operating in nature. We will first look at a Neighbor Tit-for-Tat in territorial birds, involving Dear Enemy relations. Many animals show interesting cooperation when dealing with predators. Predator inspection behaviors could reflect a tit for tat. An alternative for such behaviors is the selfish herd hypothesis, which we will also explore. Finally, simultaneous hermaphrodites and reciprocal fertilization presents a unique example of tit-for-tat, in which the fitness costs and benefits of cooperation are tightly related to fitness.
Neighbor-Stranger Recognition and Tit for Tat in Birds

Are there examples of TFT and the iterated prisoner’s dilemma in the animal kingdom? We will first look at neighbor-stranger relations in birds and the basis of the dear enemy relationships. The evolution of TFT is contingent on a number of other behaviors, such as individual recognition of partners in cooperation. Territorial neighbors have the demonstrable cognitive capacity for recognition. In the dear enemy situation it is thought that the neighbors have some sort of status quo in effect. Don't whack my back. I won't whack yours. What happens when one neighbor breaks such conventions (a non-aggression pact if you will), and invades the other male’s territory?

Rene Godard (1993) has used the power of the audio playback experiment to test whether such "defecting" neighbors are treated differently after the incursion. She played the songs of neighbors on the territory boundary where both the neighbor (N) and strangers (S) should reside. In addition, Godard played the song of the neighbor on the other side of the territory (XN), a place where the neighbor had no "right" to be. After such wrong-place incursions, the territory holder usually became much more aggressive at the boundary of the neighbor than if the playback occurred in the proper place. The targeted bird went to the neighbors border and sang aggressively in a kind of TFT response to the XN intrusion. For several days after the incursion the target bird sang at an increased rate at the border of the suspect neighbor.

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Lee Dugatkin has explored the iterated prisoner's dilemma game in a curious behavior found in fish -- predator inspection. The scenario is as follows:

1. Two fish swim side by side.
2. One moves first and leap frogs the other by a body length or two towards the predator for a closer look,
3. The other cooperates and moves forward another body length or two,
4. They continue in this fashion until they have both inspected the predator to their satisfaction.

The risks in of defection and being the recipient of the sucker's payoff are extreme. In this photo the bass attacked the inspectors. Thus the sucker's payoff could be death.

Why on earth do they do this behavior?

Is it a true tit for tat?

Dugatkin tested a number of alternative hypotheses in addition to tit for tat:

- the dilution effect,
- the selfish herd.

The dilution effect would be a tendency in prey to group together in large numbers and overwhelm the feeding capacity of the predator. At least some prey would survive.

The selfish herd is another idea we can attribute to W.D. Hamilton. Hamilton modeled the behavior of prey using the simple rule:

1. prey found on the inside of a clump will tend to survive, those on the outside are eaten.
2. Hence prey constantly jockey for the inside of a clump and appear to herd, flock, or school in a coordinated fashion.

Dugatkin ruled out these competing hypotheses and used mirror experiments to test tit for tat of an individual against itself as well as with live conspecifics. Guppies are capable of recognizing and remembering their partner's behavior and employ tit for tat-like strategies over the course of many inspections.

Simultaneous Hermaphrodites and Tit-for-tat egg exchanges

The problems faced by simultaneous hermaphrodites extend to the case of the prisoner’s dilemma considered in Chapter 8. An interesting example of egg trading is found in fishes, the only known class of vertebrates to exhibit simultaneous hermaphroditism. A few species of fish are simultaneous hermaphrodites, but these species are only found in deepwater and thus behavioral observations are quite difficult. Sea basses are found in shallow water and have been investigated extensively by Fisher (1984; 1988).

In the late afternoon, individual sea bass pair up and begin an alternating series of courtship displays. The last fish to display is the first to release eggs, but only a small packet of eggs, not its whole clutch. The partner then releases sperm to fertilize the eggs. The first fish to release the eggs then waits for the other fish to release a batch of eggs. The two fish will then continue in an alternating fashion until several batches of eggs are fertilized. One partner initiates egg laying, while the other gives sperm. They then swap. This may seem normal, but there is another completely logical way to accomplish fertilization. The first fish could simple lay its entire clutch of eggs and have the second fish fertilize it with its sperm. The second fish should then lay its eggs, and let the first fish participate in the role of male.

However, under the second scenario, the temptation to cheat is actually quite large. Sperm are far cheaper to produce than eggs. A normal male, one who does not produce any eggs, could get a lot of eggs fertilized by
suckering in the hermaphrodites to parcel their eggs out. Why not cheat and produce sperm, but fail to parcel out eggs? Under the first scenario, the egg-trading behavior observed in sea bass would greatly reduce the tendency to cheat because a cheater, one that provides sperm but no eggs, would then get just a portion of a fishes clutch if the other retaliates. Behavior of sea bass is reminiscent of an iterated cooperative game such as the prisoner’s dilemma (see Side Box 8.2). Each fish only parcels out a small quantity of eggs so that it too can use sperm it has produced with a partner that cooperatively provides eggs. Are sea bass caught in a tit for tat?

The intriguing aspect of sea bass behavior that is highly suggestive of a TFT prisoner’s dilemma is that they appear to be able to recognize partners that have cheated on them in the past. In particular, black hamlets (*Hypolectrus nigricans*) and chalk bass (*Serrannus tortugarum*) retaliate in a reciprocal fashion against past cheaters (Fischer 1984; Fischer 1986). Individuals who had a partner cheat on them in the past waited significantly longer to parcel out eggs with the cheater compared to partners that had been cooperative in past interactions. Species of bass reciprocate against cheaters.

The PD arises when:

Temptation > Cooperation > Mutual Defection > Sucker's Payoff,

or couched specifically in terms of the hermaphrodite reproductive strategies: only produce sperm>mutual fertilization>no one parcels eggs>loses sperm

Table 9.1. The pay-off matrix for tit-for-tat egg exchanges among sea bass could reflect a case of the prisoner’s dilemma. While behavioral observations are consistent with the game, additional data on the fitness consequences of an egg initiator adopting each strategy needs to be verified with experiments.

<table>
<thead>
<tr>
<th>Egg Initiator</th>
<th>Coop</th>
<th>Cooperation-all eggs fertilized by both partners.</th>
<th>Sucker's payoff gets eggs fertilized but does not get to use its own sperm, which is wasted.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cooperate</td>
<td>There is a Temptation to just produce sperm and lots of it. There are a lot of sucker’s out there in the population.</td>
<td>Mutual defection: Nobody parcels eggs. Nobody ejaculates sperm. Nothing ventured, nothing gained.</td>
<td></td>
</tr>
</tbody>
</table>

Cooperative egg spawning and fertilization also occurs in lower invertebrates. The case of the flatworm described above indicates that even a simple nervous system is capable of evolving mate discrimination and mate assessment behaviors. A hermaphroditic polychete worm, *Ophryotrocha diadema*, appears to exhibit alternating egg-laying behaviors reminiscent of a TFT (Table 9.2, (Sella 1985; Sella 1988; Sella 1991; Premoli and Sella 1995; Sella et al. 1997). Potential cheaters are common in the population in the form of males that only produce sperm. *Ophryotrocha diadema* has a protandrous phase, in which an individual worms first develop as a male with only the capacity to produce and transfer sperm. Individuals that are younger and smaller in body size benefit by first maturing as a male, because sperm is relatively cheap to produce compared to eggs. In addition, egg production is typically a function of body size in indeterminate growing invertebrates such as polychaetes. Older animals would thus be larger and the protandrous male individuals will eventually begin to produce eggs at a later age and larger body size. Individual ‘males’ in the protandrous phase could readily cheat by exploiting hermaphrodites. Safeguards against cheating by a non-reciprocating partner, either male or hermaphrodite, have evolved and protandrous males are often discarded as mates because they are unable to reciprocate with eggs. The mean number of egg masses laid by individual hermaphrodites paired with the protandrous males was significantly lower than the number of egg masses laid by hermaphrodites paired with other hermaphrodites. Hermaphroditic *O. diadema* also time their own spawning activity according to the sexual orientation of their partner and withhold egg
laying more often when the partner is protandrous. Evidence of reciprocity and egg-trading in an animal as simple as a polychaete worm is fascinating, but likely arises from a simple behavioral algorithm.

Table 19.5 Spawning between five pairs of *Ophyryotrocha diadema*, a simultaneous hermaphrodite, were remarkable with respect to their alternation of egg-laying roles. The presence of two phenotypes that lay W (white eggs) or Y (yellow) allowed Sella to distinguish which worm had laid a batch of eggs on any particular day. (after Sella 1985)

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Mutualistic Benefit and Cooperative Defense

Not all cooperative interactions necessarily involve animals in the metaphorical prisoner’s dilemma. In chapter 7, we discussed mutualistic associations in which both parties enter into a win-win situation. Cooperation can be the highest paying strategy under the three conditions: 1) individuals face a low probability of success alone, 2) an individual has a low probability of replacing a partner, and 3) the partners face a large number of interactions before the end of the association. In the latter case, the temptation to defect may not yield the highest payoff (e.g., Temptation > Cooperation) because the defector is losing a resource that is hard to find. It may be quite difficult to replace the partner with a new one (condition 2), and thus cooperation has a higher payoff than defection. The individuals are involved in a mutualism in which cooperation is the highest yielding payoff. Lima (1989) refers to the three conditions as leading to mutual dependencies in which an individual’s payoff depends heavily on cooperation from other members.

Figure 19.1 A male lion attacks a stuffed lion after hearing the recorded roar of the ‘intruder’. Lions, like most animals, seem to respond in a stereotypic fashion to such dummies. (from Grinnell et al 1995).

Maile lions, *Panthera leo*, of the Serengeti may fit the bill for a mutualistic coalition where two or more unrelated male lions team up to take over a pride of females. Once the coalition has usurped control of the females, the males participate in cooperative defense against other rival coalitions that threaten their ‘reign’. Grinnell and colleagues (1995) considered three alternative hypotheses regarding the forces that bind the coalition together: kin selection, iterated-TFT prisoner’s dilemma (see Side Box 9.2), and mutualism. They set up speaker playback experiments in which recorded roars from solitary intruders and multiple intruders show up on the coalition’s territory in the form of stuffed intruders.

The male lions readily attacked the stuffed intruders (see figure 8.33). However, males were very sensitive to asymmetries in perceived RHP of the intruding coalition relative to the coalition’s RHP. If the playback included more lions than the coalition, the coalition did not attack promptly, but waited longer to attack. Conversely, as the number of males in the defending coalition increased, the latency for the lions to attack dropped dramatically. Female lions also appear to be sensitive to acoustic asymmetries in RHP in speaker playback experiments, and are less likely to attack the speakers if the number of different roars is larger
than the defending group (McComb et al. 1994).

Males in a coalition were no less likely to attack the dummies or the speakers if they had kin or non-kin in their coalition. Kin selection is unlikely to account for the differences in the lions. Likewise, if lions were involved in an iterated prisoner’s dilemma they might be expected to base their short-term responses on their coalition partner’s response. This was not the case, suggesting that a TFT does not seem to influence an individual’s decision. Grinnell et al (1995) argue that defection by a male during an inter-coalition encounter could lead to the forfeiture of his entire lifetime reproductive success. Male coalitions are typically resident in a pride for 2-3 years and are very unlikely to regain residence if evicted. There should be no temptation to defect during an outside challenge. Male lions appear to follow Lima’s (1989) mutual dependencies model in which cooperation has a higher payoff than the temptation to defect.

Scheel and Packer (1991) applied similar logic to the phenomenon of group hunting among female lions (see Chapter 7 for background on this system). Lions were most likely to be cooperative when C, the payoff from hunting communally is greater than T, the temptation to defect, thus allowing the group to hunt without them. The conditions for C > T typically occurred when the prey was very large, and group cooperation was necessary to take down the prey. Lions also exhibit extreme division of labor in which some lions stalk from the left, and others hunt from the right (Stander 1992). As might be expected from a social animal, lions have a high degree of cooperation that not only benefits kin, but can extend to non-kin through mutualistic alliances.

**The Evolution of Sociality and Eusociality (A brief review)**

The evolution of eusociality is the most extreme form of animal societies in that members of the colony sacrifice reproductive opportunities. Eusociality is found in systems that do not have haplodiploidy such as naked mole rats.

We will explore the evolution of animal societies in greater detail. We will see that harsh conditions in the environment, which establish new breeding pairs or groups, will favor the evolution of sociality with regards to cooperative breeding. Relatedness may contribute to the evolution of sociality.

**Ants, Bees and Termites**

Consider the actual measures of relatedness in bees relative to the theoretical maximum of 0.75. Many species show estimates of relatedness far less than 0.75 and in some cases it is less than 0.50.

1. This implies that a single queen mates multiply, and thus the sisters of a colony are really half sibs, or
2. the queen shares her reproductive roles with other females in the colony.

Thus, haplodiploidy does not invariably lead to high degrees of relatedness.

Consider termites, which form colonies very similar to ants in their extreme worker specializations. Termites have warrior castes with spray nozzles similar to ants, and there is a single bloated, egg-laying queen in the termite colony that produces all the eggs.

Such a system could indeed have much higher relatedness if individuals breeding in the colony practiced brother-sister mating or mother-son matings. Recall that such oedipal inbreeding can generate higher levels of relatedness which can rival the 0.75 of hymenoptera. Similar sib-sib inbreeding can produce progeny with relatedness=0.75. In both cases sibs normally share 1/2 of their genes, but because of the probability of identity by descent, which is 0.25, the probability of shared genetic material is 0.75. If inbreeding is not a problem then inbreeding can readily promote the evolution of eusociality. In a species that has been inbred for a long time, deleterious recessive mutations would have been purged from the population long ago, so inbred species may be prone to evolve sociality
**Naked Mole Rats and suppression of reproduction of workers**

The mole rat, *Heterocephalus glaber*, or more affectionately known as the naked mole rat, is a eusocial mammal and lives in colonies of up to 275 adults, but only a single female (referred to as a queen) and a few males are reproductive. The Damaraland mole rat, *Cryptomus damarensis*, is also eusocial and lives in colonies of up to 41 adults, but only a single female (referred to as a queen) and one or two males are reproductive. The phylogeny of the mole rat group shows that eusociality has clearly evolved twice, and that apparently solitary types are embedded within the clades of social types, thus, sociality has apparently been lost at least twice. The reproductive control of eusociality is very different between naked and Damaraland mole rats.

In naked mole rats, odor cues alone are sufficient for maintaining suppressed reproduction in non-breeding females (Smith et al. 1997) suggesting that direct contact with the dominant queen is required for maintaining females in subordinate roles. The queen and other females that are high in the dominance hierarchy have clear differences in testosterone titers, which would contribute to aggression (Clarke and Faulkes 1997). The higher-ranked females also exhibit higher levels of cortisols. Removal of a queen generates shoving contests between less subordinate queens and the winner assumes control of the colony and begins breeding. In conjunction with this role, she acquires high levels of progesterone profile indicative of ovulation. However, during the period in which the new queen is determined, many high-rank females appear to exhibit a high titer of progesterone and cortisol.

In Damaraland mole rats, non-reproductive females have very low levels of both GnRH and LH compared to the dominant breeding female. Paradoxically, if the breeding female is removed, the colony becomes reproductively quiescent rather than the expected response in which a worker assumes the role of the queen. If a breeding female is removed from the colony, LH levels of the workers is elevated, suggesting that suppression of the hypothalamic-pituitary-gonadal axis is partly lifted, however they still do not breed with colony members. This implies that fertility suppression and incest avoidance are responsible for worker suppression.
In the naked mole-rat Heterocephalus glaber(a), the reproductive physiology of both sexes is suppressed, whereas in the common mole-rat Cryptomys hottentotus hottentotus(b) incest avoidance mechanisms alone maintain a reproductive division of labor within colonies (photo by Tim Jackson).

Studies of cooperative breeding in other mammalian vertebrates are largely congruent with these observations in naked mole rats (Table 19.2). Often a combination of reproductive suppression and incest taboo are required to explain the proximate bases such reproductive skew in a colony where only a few individuals breed.

How do we assess forces that promote either of these two mechanisms? Hamilton’s equation and data on fitness are required. Before moving onto studies with requisite data on reproductive suppression and incest avoidance, let us briefly review the operation of Hamilton’s equation.

Cooperative Breeding in Birds

In the case of Florida Scrub Jays, the helpers at the nest are invariably offspring of the pair that they help. The added fitness of helpers (referred to as alloparents) is a tremendous boost to inclusive fitness (see Table 19.7). The dense territories of the jays make it next to impossible for a subordinate or young bird to establish territories. Thus, by remaining with parents, particularly young inexperienced parents, scrub jay progeny can get a 0.60x0.5=0.30 increment to their own fitness.

Table 19.6 Summary of the social and reproductive characteristics of six species of African mole-rats, compared with selected other cooperatively breeding mammals from Faull (2001).

<table>
<thead>
<tr>
<th>Species</th>
<th>No. breeders per group</th>
<th>Role of helpers</th>
<th>Insect avoidance</th>
<th>Suppression of reproductive physiology in nonbreeders</th>
</tr>
</thead>
<tbody>
<tr>
<td>Heterocephalus glaber</td>
<td>1 female/1-3 males (75/295)</td>
<td>Foraging, defense, pup care</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>Cryptomys dumerolensis</td>
<td>1 female/1-2 males (11/41)</td>
<td>Foraging, defense, pup care</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>Cryptomys h. hottentotus</td>
<td>1 female/1 male (5/14)</td>
<td>Foraging</td>
<td>No</td>
<td>No</td>
</tr>
<tr>
<td>Cryptomys sulcatu</td>
<td>1 female/1 male (7/8)</td>
<td>Foraging</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>Cryptomys aruseli</td>
<td>1 female/1 male (-/20)</td>
<td>Foraging</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>Cryptomys misconduct</td>
<td>1 female/1 male (7/1)</td>
<td>Foraging</td>
<td>Yes</td>
<td>No</td>
</tr>
</tbody>
</table>

Cooperative breeding in acorn woodpeckers and incest avoidance

Acorn woodpeckers, Melanerpes formicivorus, illustrate one of the potential pitfalls of cooperative breeding birds where progeny stay to help a colony, the probability of incestuous matings is increased. Incest avoidance, which we first discussed in Chapter 2, is defined as behavioral avoidance of matings between first-order (e.g., sibs,
parents) or other close relatives (Koenig et al. 1998). Acorn woodpeckers live in large family groups of up to 15 individuals and are polygynandrous. However, groups can also have up to 7 cobreeding males, which compete for matings, and up to three joint-nesting females, besides the primary breeding female. The adult breeding population is made up of 31% non-breeding helpers that are suppressed from reproduction (Koenig and Mumme 1987).

Two competing hypotheses could explain suppression of reproduction in helpers in cooperative breeding birds:

1) reproductive competition promotes dominants to suppress reproduction of subordinates, or alternatively,
2) incest avoidance could may cause the suppression of reproduction in the helpers.

In most cooperative breeding systems it is almost impossible to discriminate between these competing hypotheses, however, reproductive vacancies in groups of Acorn Woodpeckers allowed Koenig et al. to discriminate between these two hypotheses. A reproductive vacancy is defined to be a death of one of the primary breeders in a group. The study of cooperative breeding woodpeckers at Hastings Reserve in California is one of the longest studies on cooperative breeding in existence, with detailed pedigree information now available from microsatellite based DNA fingerprinting (see Chapter 2) and behavioral observations on copulations.

The first three natural history details to establish is the frequency of extra-group mating, intra-group mating by breeders and helpers, and the overall level of incestuous breeding. If female breeders (or male breeders) mate outside of the group at a high rate, there is no problem because members of different groups are less likely to be related. Parents are unlikely to mate progeny or other kin within the group if they choose mates outside a group. The frequency of inter-group mating is in fact extremely rare (<1% based on 282 progeny, Koenig et al. 1998). The second key natural history detail to establish is whether helpers do in fact breed, and if so do they breed incestuously. Koenig et al (1998) could exclude male helpers as potential parent in 98.9% of the progeny reared by a group, and female helpers were excluded at a rate of 99.3%. Helpers do not breed within the group. With this DNA evidence they could also compute the probability of incestuous mating at 0.4% (3/744 progeny), an extremely rare event.

Next they addressed the two key competing hypotheses listed above. Is suppression due to reproductive competition versus incest avoidance? Koenig et al. (1998) turned to the data on reproductive vacancies. The key to this argument is assessing whether helpers are the same or different sex, as the sex of the reproductive vacancy. Groups have a very equal sex ratio of breeding pairs.

In the case of the incest avoidance hypothesis, the group would benefit from recruiting a breeder from outside the group while the helpers would still benefit from rearing half-sibs. The alternative to this is that the same sexed helper that could fill the role of the vacated breeder began breeding and thus elevated the risk of incest for the group and thus, elevated levels of inbreeding depression (see Chapter 12 for the costs of inbreeding depression). The majority of the vacancies were actually resolved by recruiting an immigrant (e.g., unrelated to the group) as a breeder, which was especially true for female breeding vacancies (91%). In this 66% of these cases, the female sex helpers actually dispersed before the vacancy was filled. In the case of male vacancies 64% were resolved by recruiting an unrelated immigrant, and 100% of the remaining male helpers dispersed before the vacancy was filled. The opposite side of this coin is that male helpers were more likely to stay if the reproductive vacancy was female and female helpers were more likely to stay if the reproductive vacancy was male. These helpers that stayed would actually be likely to gain copulations with the new immigrant if male begin laying eggs if they were female.

Notice, given that immigrants are preferred to fill vacancies, helpers that disperse will obtain benefits by being recruited into another group, in which case they might assume the role of breeder. Fitness of these birds can only be established indirectly, since many of the dispersing individuals leave the study plot. Data on breeding provides direct fitness inference on helpers that stay after a reproductive vacancy (Table 4).

Both male and female helpers that stay after a reproductive vacancy of the opposite sex obtain much higher fitness than helpers that stay after a reproductive vacancy of the same sex (Table 4).
In summary, most of the data support the incest avoidance hypothesis. Very little of the data support a role for reproductive competition. There are few actual fights for the vacated slots, by helpers of the same sex, rather they appear to voluntarily leave and disperse. The only potential for reproductive competition is likely to be the rare cases in which incest was actually observed and this is rare (<1%). Thus, while reproductive competition may influence some of the decision making, the scope of its overall fitness effects on success of groups (or individuals) is minor compared to the driving role of incest avoidance. Moreover, Koenig et al. (1998) clearly demonstrate that helpers are able to inherit a territory and breed following the disappearance of a related adult of the opposite sex, but not the same sex.

Seychelles warbler helpers and adaptive sex ratio modification

Additional control that a breeding pair might exert over the composition of the group can be explained with the example of Seychelles warblers, Acrocephalus sechellensis, which derive benefits from kin, but these benefits are contingent on territory quality. Seychelles warblers are found on the Seychelles archipelago in the Indian Ocean and live at very high density. Densities of breeding pairs are so high that it is virtually impossible for a newly fledged progeny to disperse and set up their own territory. Most chicks simply settle on the parent’s territory and help in the rearing of young, serving as alloparents. They supply food and incubate eggs. The impact of these alloparents varies as a function of the territory quality, which can be indexed by measuring the biomass of insects in traps (e.g., a one day estimate). On low quality territories, these alloparents might be able to help in the rearing of the young to fledging, but low food input due to sibling competition causes the extra alloparents to reduce survival of young to one year of age. However, on high quality territories the alloparents help in rearing young to fledging and in the survival of young to one year of age. Nevertheless, a 5th helper can tip the balance and begin to reduce fitness on high quality territories. The key to understanding the adaptive solutions that Seychelles warblers have at their disposal is to realize that all the helpers are female progeny.

<table>
<thead>
<tr>
<th>Sex of helpers/vacancy</th>
<th>Bred</th>
<th>Did not breed</th>
<th>Do not know</th>
<th>% that bred</th>
<th>P value*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Females:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Individuals</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male replaced; breeder female remains†</td>
<td>6</td>
<td>1</td>
<td>0</td>
<td>85.7</td>
<td>.004</td>
</tr>
<tr>
<td>Female vacancy; breeder male remains</td>
<td>1</td>
<td>9</td>
<td>3</td>
<td>10.0</td>
<td></td>
</tr>
<tr>
<td>Groups</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>.002</td>
</tr>
<tr>
<td>Male replaced; breeder female remains†</td>
<td>5</td>
<td>0</td>
<td>0</td>
<td>100.0</td>
<td></td>
</tr>
<tr>
<td>Female vacancy; breeder male remains</td>
<td>1</td>
<td>9</td>
<td>3</td>
<td>10.0</td>
<td></td>
</tr>
<tr>
<td>Males:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>.03</td>
</tr>
<tr>
<td>Individuals</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Female vacancy (observed)</td>
<td>5</td>
<td>10</td>
<td>54</td>
<td>33.3</td>
<td></td>
</tr>
<tr>
<td>Female vacancy (expected)</td>
<td>7.97</td>
<td>7.03</td>
<td>...</td>
<td>53.1</td>
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<tr>
<td>Groups</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>...</td>
</tr>
<tr>
<td>Female vacancy</td>
<td>5</td>
<td>1</td>
<td>33</td>
<td>83.3</td>
<td></td>
</tr>
</tbody>
</table>

Table 19.6. Reproductive status of workers that remained following a reproductive vacancy (from Koenig et al. 1998)
As a breeding pair adds progeny to the nest, they do so by first adding female progeny to the nest, until they have saturated their own territory with female helpers. Thereafter, they shift over to male progeny, which disperse from the natal nest to attempt to carve out a territory at some future breeding cycle.

The Sex ratio is also distorted as a function of territory quality. For example, no helpers are the optimal group size for low quality territories (Fig. 19.3) and breeding pairs tend to produce only sons on low quality territories (Fig 19.4), while on high quality territories they tend to produce daughters if only 1 helper is present. Once they reach two or more helpers on even the high quality territories, they shift over to son production (see data for 1995).

Komdeur et al. (1997) also had opportunity to test the plasticity of sex ratio adjustment. In 1988 and 1990, they transferred pairs on low quality territories from the densely population island of Cousine to Aride, which had no breeding pairs at that time. These pairs settled on high quality territories and immediately began to lay daughters, thereby producing helpers in rearing their progeny.

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Socially Mediated Speciation

The previous examples of speciation process invariably involve fitness effects that arise from ecological or genetic factors (e.g., hybrid unfitness), not purely social factors. Numerous studies have considered how ecological selection can drive reproductive isolation through assortative mating and hybrid unfitness. In these models, an individual's fitness is determined by interactions between its phenotype and the environment. Many species are however social and individual fitness in these systems is influenced by direct interactions between phenotypes.

Figure 19.5 The social interactions in Hamiltonian social space are classified by the costs (−) or benefits (+) to the actor, and costs (−) or benefits (+) to recipients.

Social Acts

- **Mutualism**
  - Actor +
  - Recipient +

- **Selfishness**
  - Actor −
  - Recipient +

- **Spite**
  - Actor −
  - Recipient −

- **Altruism**
  - Actor −
  - Recipient +

Under certain conditions, spatially restricted or viscous interactions (e.g., low dispersal) between individuals are conducive to the evolutionary maintenance of altruistic behaviors where a player donates to a recipient at a cost to itself. Defectors and cheats are potential hazards to honest altruistic donations and theory predicts that discriminatory behavior based on phenotypic differences such as greenbeard tags will be selected to avoid costly non-reciprocal donations. Hochberg et al. (2003) hypothesized that the viscosity of the very social systems that favor altruistic behaviors should, in turn, promote assortative mating between like phenotypes, with pre-mating reproductive isolation (tribal formation) as a possible end-product. Altruism is just one of many possible social acts and they also investigated how spiteful, selfish and mutualistic behaviors could influence patterns of tribe formation (Figure 19.5 and 19.6).

Figure 19.6 The value of cost and benefits that promote the formation of tribes. Tribe formation is only possible with altruistic and selfish acts (e.g., red or orange color has a high probability of speciating or forming a tribe), not spite or mutualism (light yellow).

Hochberg et al. (2003) employed a simple cellular automata model (see Side_Box on cellular automata) to show that social selection can lead to reproductive isolation. The evolution of social discrimination causes phenotypically similar individuals to congeal into different, spatially
distinct tribes. Tribal formation is only obtained, however, for certain types of social behavior: altruistic and selfish acts can produce tribes, whereas spiteful and mutualistic behaviors never do. Moreover, hybrid unfitness at tribal borders leads to the selection of mating preferences, which then spread to the core areas of the respective tribes. The boundary between tribes are stable because alternately tagged individuals that mate together have low fitness (their progeny will donate to the wrong tribe in future generations), compared to individuals that mate within their own tag color (e.g., and keep the social act only occurring within the tribe and not across tribes). Unlike models of resource competition, their model generates reproductive isolation in an ecologically homogeneous environment, but socially heterogenous environment.

**Altruism act rule**  
\[ T_s \]  
++ 0 0  
++ Barrier to gene flow  

**Thievery act rule**  
\[ T_{ns} \]  
0 0  

Under an altruistic act rule, net cooperation (+ +) reigns within tribal centres and interactions are avoided at the borders, where contact occurs between tribes. However, with selfishness (thievery), net antagonistic behaviors (- -) are suppressed in homogenously tagged regions yet expressed in border zones. However, they found that the evolutionary path to these net interactions is only attained under altruistic and selfish act rules; tribal formation did not occur if social acts were spiteful or mutualistic. Given mutualistic interactions, indiscriminate use of the behavior is favored, as any interaction brings the actor a net gain, and this promiscuous social behavior is susceptible to cheaters. In contrast for spiteful interactions, total suppression of the behavior is favored as any interaction results in a net loss to the actor and thus no social interactions evolve. In either case, the evolution of social discrimination is suppressed, barring the establishment of coherent tribes.

Figure 19.7 An example of culturally transmitted songs in parrots of central and South America. Highly advanced social behaviors used between breeding pairs might generate the forces necessary for socially mediated speciation. This is because mating system dynamics that involve rearing of young and biparental care are a form of mating system cooperation that is susceptible to cheater strategies on the part of one breeding partner (e.g., often the male in a pair). Cheating need not be involved if successful rearing requires highly coordinated signals that vary among areas due to “cultural drift”. Incompatible signals for coordinating a breeding pair might be mismatched between diverging cultures.
The social interactions and the patterns identified by Hochberg et al. (2003) are potentially important in systems with repeated acts between individuals, such as sessile (Macnair and Gardner 1998; Grosberg and Hart 2000; Shoemaker and Ross 1996), territorial (Temeles 1994), or long-lived (Barbujani and Sokal 1990) organisms. For example, avian song is used in tag-based identification between territorial males (Baker et al. 1981; Godard 1993) and song is also employed by females during mate choice to identify local males (Baker et al. 1981). Dialect differences might have arisen by the mechanisms that they describe (see Figure on Parrots, below) or the examples on vitiine finches (Chapter 17).

Tag divergence may also occur in organisms with chemically-based recognition such as social insects (Keller and Ross 1998). For instance, many ant species use chemical cues for recognition and colony similarity may promote cooperation between colonies with similar tags but divergence between those with alternative tags (see greenbeard that is described in Chapter 4 for fire ants).

RPS mating systems (see chapter 9) have important implications for speciation. Interplay among positive FDS in both sexes and negative FDS is clear in the context of RPS mating systems. Positive FDS in the lizard RPS is the result of cooperative behavior (Sinervo & Clobert 2003) not merely positive FD mate preference. Signaler-receiver relations of

Figure 19.9 (A) Results from a simulation model of socially mediated speciation (Hochberg et al. 2003) with fitness payoffs (measured in nature, Sinervo et al. 2006b; Sinervo & Clobert 2003) from rock-paper-scissor (RPS) cycles of side-blotched lizards superimposed. The speciation model indicates that reproductive isolation is likely (orange-red) when alternatively tagged altruists that donate to self, or usurpers that take from nonself, interact on spatially structured landscapes. Speciation is unlikely (yellow) for mutualistic or spiteful social interactions. (B) The RPS mating system traverses these social domains during the five-year cycle (superimposed on panel A): B altruists are invaded by O (Sinervo et al. 2006a); when O becomes common, O altruists must disperse and pay costs of dispersal (Sinervo & Clobert 2003; Sinervo et al. 2006ab); Y selfishness invades O, and B mutualists invade Y, driving the system to a point where O can reinvade. Thus, the lizard RPS mating system is susceptible to processes of socially mediated speciation: B females exhibit self-preference for B sires (Sinervo et al. 2006b) and B male cooperation also generates positive FDS. For example, elimination of Y should fix the system on B and O or on B alone, a system of true altruism. (C) Socially mediated speciation may have arisen from negative FDS on Cichlids. Left panel: Representative “blue” and “yellow–red” male nuptial-color types of two species of Lake Victoria Cichlids: Lithochromis rubripinnis (top) and Lithochromis spp. “red dorsum” (bottom). Right panel: two nuptial-color morphs from a single population (Makobe Island) of Neochromis omnicaeruleus. (D) Under-representation of a territory owner’s own coloration among the males that occupy adjacent territories. White bar, the mean ratio \( n^* \) (“red tail”)/n (“blue tail”) among territorial males on a spawning site (256 m²) at Makobe Island (Lake Victoria). Gray bars, the same ratios among territories adjacent to territory owners with a “red tail” (Neochromis rufocaudalis) or a “blue tail” (N. omnicaeruleus) (C–D Seehausen & Schluter 2004).
cooperation and sexual selection share many runaway properties because both promote a buildup of genetic correlations among signalers and receivers. Recent gene mapping studies (Sinervo et al. 2006b) indicate that genetic factors for male self-recognition and the OBY color signal locus, named for the throat colors orange, blue and yellow, generates true greenbeard altruism (Sinervo et al. 2006b). When orange-throated male despots invade the cooperative blue-throated strategy, the blue allele confers an altruistic benefit among unrelated blue males: blue males next to orange lose competitions for paternity to the orange, but this altruistic male buffers his unrelated territorial partner from orange male aggression. In contrast, when cooperative blue males invade yellow the blue alliance is mutualistic. Thus, RPS social dynamics drive an evolutionary cycle of altruism and mutualism (Figure 5a and 5b).

Altruism exhibited in RPS systems may also predispose such mating systems to socially mediated speciation (Hochberg et al. 2003), a theory of speciation involving FDS and social behaviors like true altruism (Figure 5a). This is because the same genetic factors governing blue male self-recognition are also expressed in females and drive mate preference (Sinervo et al. 2006b), a form of positive FDS for self-mating. The dual action of positive FDS in mating and male-male cooperation may rapidly eliminate strategies other than blue (Figure 19.9a). Speciation requires both assortative mating and hybrid unfitness. Hybrid unfitness arises under social selection because self-recognition loci and loci that promote cooperation are distributed across the genome (Sinervo et al. 2006b); any mixing of this variation with alternative strategies such as usurpation (orange) or parasitism (yellow) breaks up the coadapted gene complex of cooperation.

In this regard, self-recognition of either true or kin altruism may parsimoniously arise from the MHC (Aeschlimann et al. 2003, Grosberg & Hart 2000, Landry et al. 2001, Potts et al. 1991, Reusch et al. 2001). Thus, MHC self-recognition may, in some social systems, serve as a key signal-recognition complex that maintains coadapted gene complexes of social behavior. However, selection favoring self-mate preference produces self-similar progeny, which should tradeoff with the nonself mating benefits of MHC in the context of disease resistance (see above). Although links between the positive frequency dependent selection (FDS) of sexual selection and speciation have been made (Lande 1981), the explicit role of negative and positive FDS of social systems and speciation has received little empirical attention (however see Seehausen & Schluter 2004, described in Figure 19.9c), even though mating system examples and theory (Dieckmann & Doebeli 1999, Hochberg et al. 2003) suggest an important role in diversification. Self- versus nonself-recognition systems like MHC may underlie self-mate preference at hybrid zones between species where reproductive isolation is forming (Howard 1999). Similarly, memetic forms of self-recognition, such as song imprinting among male and female Vidaune finches and their host species, provide analogous social avenues for speciation that involve interplay between cultural and biological evolution.

Indeed humans use many social tags including language, dialects, and even religion to identify individuals for social acts (positive and negative). Perhaps tribe formation in humans follows similar rules of social speciation. In the next Chapter, we explore the evolution of human consciousness and the rules that may have been used by ancient human societies in tribe formation. These rules are codified in the origins of language, art, and even other cultural systems like religion. In chapter 20 we tackle the interesting problem of the biological origins of cultural phenomena of humans.
Side-box cellular automata

Haploid Sexual Model -- free recombination
1. Grid of cells wrapped over a torus
2. There are two “tags” in the system
3. Random mortality occurs and vacant cells are colonised by the progeny of the neighbour with the highest social fitness
4. Social fitness is the net effect of neighbours less the costs of interacting with neighbours. Two independent “acts” occur between any pair of players

A cellular automata is a grid of interacting organisms which follow very simple rules of interaction (e.g., behaviors). The goal in such cellular automata modeling is to come up with pattern out of homogeneity. The formation of tribes subject to three loci: social act locus, mate choice locus, and tag-based identification generate alternative tagged (e.g., red or blue) groups of individuals that are altruistic within their own social group.

Players at each cell have an allele for the following three loci:
1. a tag (red or blue)
2. genes for mating rules (prefer self, non-self, random)
3. a gene for social acts (see text).

Study Questions for Social Evolution
1. Distinguish between kin altruism (selection) and true altruism. What are the critical conditions for the evolution of true altruism?
2. What is the prisoner's dilemma? A payoff matrix or a discussion of the rewards and punishments involved is essential.
3. What is reciprocal altruism? What conditions favor the evolution of reciprocal altruism based on a consideration of iterated tit-for-tat and the prisoner's dilemma?
4. How does the model of mutual dependency differ from the model for the iterated PD as an explanation of the evolution of cooperation (hint: how are the relative values of the payoffs critically different)?
5. Describe two biological examples of tit-for-tat, and describe how each example satisfies the critical conditions for altruism listed in number 1.
6. Distinguish between social and eusocial associations. How are naked mole rats similar to eusocial insects? What controls the caste development in ants and bees? What controls caste development in the naked mole rat?
7. Describe evidence for suppression of reproduction by dominants. Describe evidence for suppression of reproduction by subordinates due to inbreeding avoidance. (Your answer can be drawn from Eusocial or helper social systems).
8. Why is it difficult to explain the evolution of cooperation in animals? (By "cooperation" I mean an act that occurs between two unrelated individuals that is mutually beneficial). Discuss your answer in terms of the levels of selection. Which theory explains the evolution of cooperation and why is it a satisfactory explanation? (You can discuss more than one theory).
9. What are the two forms of cooperation?
10. Outline the elements of a theory of socially mediated speciation. What generates hybrid unfitness? What generates assortative mating?