Web Topic 13.1
Direct Benefit Models of Cooperation

Introduction

Why humans should or do cooperate has been of concern to philosophers and economists for millennia. Humans often engage in extensive cooperation with unrelated individuals showing that kin selection and greenbeard biases are not necessary to compensate for the costs of being a cooperator. This immediately raises the question of whether the same mechanisms might explain the many cooperative interactions seen in other species; at minimum, kin selection cannot explain cooperative mutualisms between different species. In this Web Topic, we introduce the evolutionary game models advanced to explain cooperation without genetic compensations, and note particular cases that may be relevant to animal communication. Because the literature on this topic, especially that dealing with human cooperation, is so extensive, we can barely do justice to it here. However, we provide some further reading sources at the end of the module that provide gateways to this larger literature. Readers of this module should be familiar with the classification of evolutionary game models and the logic of “take” and “give” games reviewed in Web Topic 10.5.

Defining and classifying cooperation

A necessary condition for cooperation is that at least one individual undertakes an action at some cost to itself and other individuals benefit from the first individual’s investment. The first individual’s action could have been prompted by likely compensating benefits to itself, or its efforts might have been “purloined” as the result of theft, deceit, or coercion (Connor 1995). Setting coercive manipulations aside for the moment, there are a number of ways that a cooperative interaction could generate net benefits for both parties. In this module, we will also ignore genetic benefits as a result of kin selection or greenbeard biases: our focus here is on cooperation among unrelated animals, or at least, on contexts in which relatedness makes no significant contribution to the cooperation economics. These are usually called the “direct benefits of cooperation” (Bergmüller et al. 2007; Leimar and Hammerstein 2010).

Consider an animal B that is pursuing some direct benefit to itself. There are three ways that animal A might interact with B with net positive benefits to both parties and without either party invoking coercion or deceit:

- **By-Product Mutualism**: In the simplest case, animal A puts itself sufficiently nearby or ensures that it is sufficiently connected to animal B that animal B’s efforts not only benefit animal B but also provide some spill-over benefits to animal A. This is called by-product mutualism (West-Eberhard 1975; Brown 1983). In these cases, A benefits by B’s actions without altering the costs or benefits experienced by B. By-product mutualism can be one-sided or two-sided: in the latter case, each of A and B pursues its own goals, but they coordinate their actions so that each party receives some by-product benefit through the actions of the other. This two-sided option is called coordinated by-product mutualism.

- **Pseudo-reciprocity**: Again suppose that animal B is pursuing its own selfish activities, but animal A, instead of remaining passively on the sidelines, expends some cost to help animal B achieve B’s selfish goals. Again, animal A receives by-product benefits from B’s actions, but perhaps because of its investment in B’s efforts, it might receive more or different benefits. This is called pseudo-reciprocity (Connor 1995; Leimar and Connor 2003; Connor 2007). Since A can vary the size and nature of its investment, and its strategy can affect the payoffs for B, this interaction can be formulated as a game and ESSs sought (Leimar and Connor 2003). Note that given its definition, pseudo-reciprocity includes most animal communication as a special case: the receiver is faced with a decision about future states or actions and the sender provides information that facilitates that decision in a way that benefits both parties. Note also that, as with the prior case, both parties might coordinate pseudo-reciprocity with the other (mutual pseudo-reciprocity).

- **Reciprocity**: In the third case, animal B again pursues its own interests, and animal A suffers some costs to help animal B in that pursuit. However, in this case, there is no immediate spill-over benefit to animal A. The only way A can recoup its cost and achieve a positive payoff from its actions is if A and B subsequently exchange roles.
such that B pays costs to provide benefits to A. The key difference between pseudo-reciprocity and reciprocity is that benefits accrued by the recipient in the former spill over on the donor without the recipient changing its role, whereas roles must be exchanged before both parties achieve net positive payoffs in the reciprocity case (Trivers 1971).

![Figure 1. Criterion tree for classifying types of cooperation among unrelated animals.](image)

Combining these three alternatives with possible manipulation, several authors have proposed criterion trees for assigning real examples to categories. One example is shown in Figure 1. Where the party invested in by animal A is the same one who delivers the consequences to animal A, the exchange is said to be direct; if the feedback on animal A comes from a third party, the exchange is said to be indirect. Manipulation, pseudo-reciprocity, and reciprocity can all lead to either direct or indirect accountings. This schema, and others like it, have proved very effective at classifying known examples of animal and human cooperation: all of the classical examples such as cooperative hunting, joint predator surveillance, cooperative breeding, and symbiosis can be assigned to their own spot in such a tree (Connor 1995; Leimar and Connor 2003; Bergmüller et al. 2007; Connor 2007; Bshary and Bergmüller 2008; Connor 2010). This partitioning has greatly clarified economic and game theoretic modeling of cooperation as different parts of the classification tree require different assumptions to generate ESSs and exhibit quite different evolutionary dynamics. One comment on terminology: some authors have lobbied for the restriction of the word “mutualism” to interspecific relationships and “cooperation” to intraspecific ones (Bronstein 2001; Bergmüller et al. 2007). In this module, we use the two terms as synonyms because such use is already widespread in the literature and because convergent inter- and intraspecific associations can occur at the same point in classification trees such as the one in Figure 1. However, readers should be alert to publications where the authors specifically restrict the term mutualism to interspecific associations.

**An overview of the basic problem**

Before we examine specific cases, it is useful to stand back and identify the challenges that the evolution of direct benefit cooperation faces from the perspective of evolutionary game theory. There are two basic hurdles that usually hinder the evolution of cooperation. The first arises because many situations in which mutual cooperation could be beneficial are vulnerable to cheats and defectors. When modeled as a single-bout 2x2 symmetric contest, the result is
invariably a take game with the Cheat or Defector strategy as the pure ESS (Figure 2A). The first challenge is thus to identify conditions under which take games can be replaced by a give games (Figure 2B). Once achieved, the second problem arises. As we saw in Web Topic 10.5, give games in the absence of genetic compensations such as greenbeard or kin selection invariably have two possible ESSs: one in which everyone cooperates, and one in which everyone defects. A few games (e.g., the Snowdrift Game discussed below) can lead to a mixed ESS in which each party cooperates some of the time, and defects the rest of the time. However, it is extremely difficult to find any realistic model in which pure cooperation is the only ESS. The second challenge is thus to find conditions that might get a population to the all-cooperation ESS and hold it there despite drift or other factors outside the basic game. While some of the literature on cooperation mingles both hurdles, an equally diverse amount focuses on only one of the two steps. We shall try to keep straight which hurdle we are considering in the following discussion.

Figure 2. Take versus give games of cooperation. (A) The normal form matrix for this example shows that it is a take game: even though everyone cooperating would produce a higher per capita payoff (pareto optimum) than everyone defecting, the advantages to defecting when others are cooperating have an even higher payoff. The result is that cooperation degenerates until everyone is defecting as the best reply. Defect is then a pure ESS. (B) In this game, pure cooperation can be an ESS, but it is only one of two possible ones, the other being pure defect—which is found depends on starting conditions. If the initial condition is for everyone to be selfish and not cooperate, the system will stay there barring drift or some other outside factor.

The prisoner’s dilemma

Most modern treatments of the economics and/or evolution of cooperation begin with the Prisoner’s Dilemma. This model was first introduced to the evolutionary biology literature by Trivers (1971). In this game, two suspects are taken prisoner by the police and held separately. Each is urged to provide incriminating evidence about the other. The relevant game is typically modeled as a dyadic single-bout 2 x 2 symmetric contest. If both keep silent, they are likely to gain only a light sentence given the lack of detailed evidence (a per capita payoff of $R$). If one provides incriminating evidence on the other, that suspect get to go free ($T$) whereas the other gets sent to jail for a very long time ($S$). If both provide evidence on each other, they both go to jail but for less time than if they had not provided evidence ($P$). In this game $T > R > P > S$. The normal form matrix for the game is shown in Figure 3.
As is clear in Figure 3, this is a classic take game in which pure Defect is the only ESS. Cooperation will never evolve even though the pareto optimum of joint cooperation yields a higher payoff than the ESS (e.g., \( R > P \)). One can imagine many other scenarios in both animals and humans that would also be characterized by this game. As we shall see below, the only way to convert the Prisoner’s Dilemma to a give game with cooperation as one of the ESSs is to alter the type of game that is considered.

**An intermediate: the Snowdrift game**

As we saw in Web Topic 10.5, a single-bout 2 x 2 symmetric contest has four possible outcomes: each of the two strategies can be the only pure ESS, both can be pure ESSs, or there may be a stable mixture of the two strategies as the ESS. The Prisoner’s Dilemma game has a single pure ESS: defect. All give games have two pure ESSs, which one is seen depends on initial conditions or if populations are finite, on relative bases of attraction. The Snowdrift Game describes a cooperation context in which the ESS is a mixed strategy (Hauert and Doebeli 2004; Nowak 2006a). The scenario begins with two commuters trapped in deep snow on the highway. If both get out and shovel snow, they can get home sooner and split the effort. However, if one lets the other do the digging, he still gets home but evades all the work. If neither shovel snow, they remain stuck. Assuming a common currency for costs and benefits, let \( R \) be the net payoff if both drivers dig and share the work equally, \( T \) be the payoff to the driver who lets the other do all the work, \( S \) be the payoff to the driver who does all the digging alone, and \( P \) be the payoff to both drivers if neither shovels. This results in the same normal form matrix as the Prisoner’s Dilemma except that this time \( T > R > S > P \). This is shown in Figure 4.
This model gets us part of the way between the take game of the Prisoner’s Dilemma and a cooperative give game, but only part of the way. In addition, it only characterizes a subset of the types of cooperation seen in nature: specifically, those in which there is a common task whose completion benefits both parties. It does not help us with situations in which the two parties do not face a common task.

Replacing the take game with a give game

As long as there are opportunities to cheat or defect, it appears impossible to get a give game involving cooperation from a single-bout contest like the Prisoner’s Dilemma. In some contexts, we might be able to find stable mixtures of the two strategies (Snowdrift game). However, we can achieve a situation in which cooperation is a pure ESS only if we change the type of game. One solution is to allow participants to interact repeatedly: if early bouts can provide information that allows players to adjust strategies, the resulting sequential game might have an ESS policy favoring cooperation that is unavailable to single-bout contexts. A second way to change the game is to replace dyadic contests with multiplayer scrambles: as we saw in Web Topic 10.5, adding more players can open up ESS possibilities not available to dyadic games. For both approaches, we begin with the assumptions that the relevant populations are infinite in size and strategies are “well-mixed” throughout the population.

- **Dyadic sequential models of cooperation.** Even when treated as a single bout interaction, reciprocity is intrinsically a sequential game. We shall focus here on repeated interactions between the same pair of players. This is called **direct reciprocity.** Direct reciprocity was initially modeled as an iterated Prisoner’s Dilemma game in which a player could elect to cooperate or defect in each successive bout depending on what had happened in earlier bouts. Axelrod and Hamilton (1981) pointed out that any such game based on a finite number of bouts was bound to degenerate into defection by both parties: the last player in an expected finite sequence will always do best by defecting; knowing this, the other player will defect in the penultimate bout, and so on until both parties defect in every bout as in the single-shot Prisoner’s Dilemma. However, if the total number of bouts is unknown, this unraveling risk can be avoided.

Unfortunately, this complicates the relevant models as there are an infinite number of possible choreographies that a player could adopt given an infinite sequence of bouts. Axelrod thus hosted a “tournament” and invited anyone to submit their favorite choreography or rule-of-thumb policy. These were then competed against each other in computer simulations. One policy that won frequently was Tit-for-Tat (TFT): a TFT player always started with cooperate, and then just did what their opponent did on the latter’s last move. If the probability that two players will interact again, \( w \), is constant, the expected payoff of using TFT against other simple policies over an infinite number of successive bouts can be calculated and these expected payoffs compared to similar calculations for alternative strategies in a normal form game matrix. For example, if the probability that two interactants will meet again is \( w \), then the probability that they meet twice more is \( w^2 \), three times more \( w^3 \), etc. Suppose a TFT player is playing against another TFT player. During each bout, both players cooperate. The expected payoff for either player over an infinite number of bouts using the same payoffs for the Prisoner’s Dilemma (\( T, R, P, \) and \( S \)) is:

\[
PO(TFT,TFT) = R + wR + w^2R + w^3R + w^4R + ... = R(1 + w + w^2 + w^3 + w^4 + ...)
\]

Since the infinite series \( 1 + w^2 + w^3 + w^4 + ... \) is convergent, it can be replaced with its sum which is \( 1/(1-w) \). Thus the expected payoff for a TFT player repeatedly playing against another TFT player is

\[
PO(TFT,TFT) = R/(1-w)
\]

A similar logic can be used to compute the average payoff to a player using a policy of always defecting (AllD) against another who also always defects:
The average payoffs for a TFT and AllD player playing against each other are a little trickier algebraically but the same infinite series can be extracted. The resulting normal form matrix for an entire infinite series of bouts is shown in **Figure 5**:

![Iterated Prisoner's Dilemma game using Tit-for-Tat (TFT) and Always Defect (AllD) as policies for sequential game with infinite number of bouts.](image)

Since by assumption in a Prisoner's Dilemma game, \( P > S \), it is easy to show that \( P(1-w) > S + wP(1-w) \), so there is always a dot in the lower right corner of the matrix. The question is then whether TFT or AllD is the best response to an opponent playing TFT. TFT is the best response only if \( R(1-w) > T + wP(1-w) \). This will be true when

\[
w > \frac{(T-R)}{(T-P)}
\]

Thus we can turn the Prisoner's Dilemma from a take game into a give game by allowing an infinite number of bouts, playing TFT against AllD, and assuming that the probability of two animals interacting again \( (w) \) is sufficient high, and/or that the difference in payoffs between cooperating and being exploited \( (T-R) \) is sufficiently small.

While this type of result at least allows pure cooperating to evolve, there are serious caveats. The first is that, at best, a give game has two possible pure ESSs—which is found depends on initial conditions. TFT thus cannot be the only pure ESS possible. Secondly, TFT and AllD are only two of an infinite number of choreographies and policies. TFT may find itself playing against any of these other strategies in dyadic contests: would it generate a give game in all cases? Third, there is no reason why only two strategies should be present: might dynamics change when three or more strategies are available (like the Rock–Paper–Scissors game)? Fourth, errors in assessing the opponent’s last move can destabilize a TFT population. Last, the classical TFT models lock each pair of individuals into long term interactions in which complex accountings must be maintained so that both parties achieve net positive payoffs. A number of authors have argued that these caveats should and do make classically defined direct reciprocity a rare process in nature (Hammerstein 2003; West et al. 2007b; Clutton-Brock 2009). Given the apparent importance of reciprocity in human interactions, a very large number of alternatives to TFT for iterated Prisoner's Dilemma games have been put forward. Some of these seem too complicated for most animal contexts; however, others (such as Win–stay/Lose–shift (also called PAVLOV) which focuses on the stability of a player's own payoffs as the sequence proceeds) are general enough that they might be widely applicable. For overviews of these modified models, see Dugatkin (1998) and Nowak (2006a).

**Multi-player Scramble Games of Cooperation**. There are two main ways in which adding more players to a single interaction can change cooperation economics:

- **Partner Choice and Biological Markets**: The first alteration is to keep interactions dyadic, but allow a player to choose its partner for any given interaction (partner choice), and decide for how many occasions it will continue to interact with any given player (partner fidelity) (Bull and Rice 1991). While this eliminates the
locked-in cumulative accounting of classically defined direct reciprocity, it imposes a new burden by requiring that players identify some suitable criteria on which to base these decisions.

One obvious criterion is the value to the chooser of the commodity or service that a potential partner has to offer relative to the value to the partner of what the chooser might provide in exchange. If the chooser can provide a rare or highly valued commodity/service, and there are many potential partners, the chooser can be highly selective and pick a partner that will give it the best deal in return. Exchanges based on such selective trades are called **biological markets** (Noë and Hammerstein 1994, 1995).

Note that the two parties need not exchange the same commodity or service: one species might offer grooming services in exchange for a sharing of food or help in mate defense (de Waal 1997; Barrett et al. 1999; Gumert 2007; Fruteau et al. 2009; Fruteau et al. 2011); males of a bird species might offer newly constructed nest sites in exchange for female matings (Metz et al. 2007); and unrelated floaters may be allowed to join a breeding group in exchange for helping to rear offspring (Gaston 1978; Kokko et al. 2002). Stable cooperative trading only requires that the net payoffs to players of similar status be of roughly equal utility (e.g., a fair trade) (Hoeksema and Schwartz 2003; Andre and Baumard 2011). The relative valuation of the commodities may be negotiated through an extended series of signal exchanges (Patricelli et al. 2011), or by the imposition of costs on the contributing player that would only be borne if the associated commodity were truly of high value (Archetti 2011). Players might also rely on personality traits exhibited by alternative potential partners (Bergmüller et al. 2010; McNamara and Leimar 2010). Players of unequal status can also engage in stable commodity/service exchanges as long as the most exploitable party retains the ability to terminate the exchange and find an alternative partner (Johnstone and Bshary 2008; Wang and Shi 2010). The freedom to seek alternatives can interact with coercion by dominants in complicated ways, resulting in a diverse mix of accountings when asymmetries are present (Buston et al. 2007).

An alternative, and not necessarily exclusive, criterion that players might use to choose cooperation partners is the **reputation** of each candidate as a reliable and effective partner. Players can rank relative reputations by eavesdropping on prior exchanges involving a particular candidate (Earley 2010), or in humans, through gossip (Sommerfeld et al. 2007; Sommerfeld et al. 2008). Players may even generate a market by competing to acquire the best reputations (Zahavi 1995; Roberts 1998). Costly investments in cooperation by an individual now may thus be repaid later not by the recipient of the original investment (as in direct reciprocity), but instead by third parties who preferentially seek out affiliations with high reputation individuals. A reliance on reputation to determine partner choice and fidelity is thus one way to generate **indirect reciprocity**. In a variety of experiments with humans, provision of information about the past generosity of fellow players leads to higher levels of sustained cooperation (Nowak and Sigmund 2005).

- **Scrambles and Public Goods Games**: The second way in which multiple players might change cooperation economics is if the relevant game becomes a scramble instead of a contest. All of the games discussed in prior section of this module are contests: they exhibit first-order frequency dependence in that the average payoff of adopting a given strategy across many interactions depends on the relative abundances of the alternative strategies; however, the payoffs for a particular combination of strategies in a single interaction are fixed. In a scramble, both the long-term average payoffs and those for a given pair of strategies during a single interaction depend on the relative abundances of alternative strategies. Situations in which members of a group contribute investments to create and maintain some common good, and all members benefit equally from that common good, are called public goods games. The payoffs both within and across bouts depend on how much each participant contributed to the public good; this game is thus a scramble. Models of public goods games vary in whether the $N$-players interact as dyads or instead as multiple players during a given bout. However, all public goods models share the assumption of multiple bouts in which players can change strategies as the game progresses.
While communal efforts might lead to highly synergistic benefits relative to what individuals might obtain on their own, a public goods game is subject to the same risks of defection that we saw with the Prisoner’s Dilemma. Consider a shared pasture, called a “commons,” in which all local farmers are allowed to graze their cattle. If everyone adheres to the same small number of cattle, they will all enjoy a pareto optimum. However, if some farmers give in to the temptation to graze more than their share of cattle on the commons, others will suffer and may retaliate by increasing their cattle numbers to restore their shares of the total. Eventually everyone will be worse off as the commons becomes severely overgrazed and nobody’s cattle do well. This is called the tragedy of the commons (Hardin 1968), and is the N-player equivalent of the dyadic single bout Prisoner’s Dilemma. It applies to many joint animal activities including cooperative hunting, joint territorial defense, cooperative breeding, and shared refuge building (Killingback et al. 2006; Bshary and Bshary 2010).

While some cases of public goods behaviors in animals might be explained as by-product mutualism or pseudo-reciprocity (Bergmüller et al. 2007; Connor 2007), many others remain at risk of a tragedy of the commons collapse (Rankin et al. 2007). What can make these types of cooperative efforts evolutionarily stable? Three additional policies have been identified that can help promote the evolution of cooperation in public goods games. Note that these need not be exclusive and some models of public good games explicitly include two or even all three practices concurrently:

- **Punishment**: In a wide variety of experiments on human public goods games, players invariably begin cooperating, but over many successive bouts, defection gradually increases and finally replaces most cooperation. If partway through the game, while cooperation is still reasonably common, players are allowed to add punishment of defectors (or in milder terms, policing), punishment is adopted increasingly as the game progresses and the game usually stabilizes at a relatively high rate of cooperation (Fehr and Gachter 2002; West et al. 2002; Boyd et al. 2003; Frank 2003; Gardner and West 2004; Gurerk et al. 2006; Sigmund 2007). Punishment is widely used throughout human societies to stabilize cooperation (Herrmann et al. 2008). One caveat that arises in relevant models is that punishment is usually costly to the punisher (Dreber et al. 2008). This sets up a potential for second-order defection in which individuals who are otherwise cooperators fail to contribute to the punishing of defectors. Second-order defection can be curbed by second-order punishers, but again, there can be defections at this level as well (Jensen 2010; Sigmund 2010). Punishment is more likely to be stable if punishers are sometimes “corrupt”: that is, they are able to extort some additional benefits given their power or they themselves quietly become defectors and reduce contributions to the public good (Ubeda and Duenez-Guzman 2011). Where overt punishment can be replaced by less costly but credible threats, this can also stabilize punishment (Cant and Johnstone 2009; Cant 2011). In the absence of corruption or existing high levels of cooperation, some other concurrent policy may be required to stabilize punishment. As we discuss below, reputation can often fulfill that role (dos Santos et al. 2011). While punishment can help stabilize an existing population of cooperators, it cannot help a rare cooperative strategy invade a population of defectors (Lehmann et al. 2007; Rand et al. 2009; Forsyth and Hauert 2011).

- **Rewards**: Rewarding cooperators is the opposite of punishing defectors. Unlike punishment, reward can help rare cooperator mutants get established in a population of defectors, but reward is not effective at stabilizing cooperation when cooperators begin to dominate in the population (Hauert 2010; Forsyth and Hauert 2011). This is probably because a punishment policy is most costly when most of the population are defectors and is needed less often when cooperators are common; the reverse is true for a rewarding policy which becomes most expensive when cooperators are common (Sigmund 2010). Thus rewards are more likely to be effective when cooperation is rare, and punishment when it is common. As with punishment, combining rewards with reputation can lead to stable cooperation, although this combination can also generate cyclic and chaotic dynamics (Hauert 2010).

- **Reputation (Indirect Reciprocity)**: The provision of reputation information often stabilizes high
levels of cooperation in human public goods experiments (Milinski et al. 2002; Nowak and Sigmund 2005; Sigmund 2010; Sylwester and Roberts 2010). One particularly interesting set of studies alternated dyadic exchanges where participants could select their levels of generosity, and public goods games where all players could elect how much to contribute to the public good. When information about the players’ relative generosities in the first stage games were made public, reputations played a significant role in stabilizing high levels of cooperation in the subsequent public goods games (Milinski et al. 2002; Semmann et al. 2004, 2005). In a sense, selective choice of partners based on reputation is a form of mild punishment: instead of overt harm inflicted on defectors, the latter are excluded from participating in future exchanges. Selective partnering using reputations is thus less costly than having to inflict physical punishment (Rockenbach and Milinski 2006; Ohtsuki et al. 2009). Despite this, humans often recruit both selective partner choice based on reputation and overt punishment in experimental public goods games. One explanation is that being a punisher might improve a player’s reputation, and this would then compensate for the costs of inflicting punishment.

A number of related models provide additional perspectives. Using three alternative discrete strategies, instead of two, results in more complex dynamics: one model includes cooperators, defectors, and punishers as separate strategies (Szolnoki et al. 2011), and another lets the third strategy be the chance to abstain from any interactions (Semmann et al. 2003). Both models can produce stable cooperation, but also Rock–Paper–Scissors-like cycles depending on parameters and initial conditions. Making the level of cooperation into a continuous variable turns the discrete games above into a continuous one: stable equilibria tend to occur at intermediate levels of cooperation (Zhang et al. 2010). Adding error in assessment of reputations or value of commodities (perhaps due to reliance on rules of thumb), can also change the evolutionary dynamics (Nowak and Sigmund 2005; Brosnan et al. 2010; de Waal and Suchak 2010; Sigmund 2010).

Favoring the cooperation ESS in a give game

The models reviewed above typically assume that focal populations are effectively infinite in size and well-mixed, so that different strategies are encountered in proportion to their global abundances. The payoff matrices for these games usually do not change if these assumptions are violated, and thus the basic outcomes (e.g., a give game) remain. What can change if one or both assumptions is violated is which of the alternative ESSs in the resulting give game is most likely to occur. Finite populations are subject to drift, and the smaller the population, the greater the role of drift relative to selection. The dynamics become stochastic, and this can significantly weaken the usual predictions.

Populations can also have heterogeneous distributions of alternative strategies; such populations are often called “structured” and modeled as networks (see Chapter 15). A well-mixed population is a network in which every individual is potentially linked to every other individual. Heterogeneously structured populations have a much more sparse network than that for a well-mixed population: only some individuals in structured populations are linked to any focal individual. There are two general classes of heterogeneous networks: a) those in which there is at least one path (however convoluted) linking any two individuals (a giant component); or b) not all individuals are linked by a path and thus the population is subdivided into multiple components.

All of the models below assume finite populations; however, they vary as to whether they focus on small population sizes where drift is significant, or sufficiently large ones where drift is not a major factor. They also vary depending on whether their structure is well-mixed, fully but sparsely linked, or subdivided into separate components. We cannot review all combinations here, but will provide a sampling of the more widely cited ones.

- **Small well-mixed populations**: This combination is nicely reviewed by Nowak (2006a). Outcomes depend in part on the strength of selection associated with the relevant game: if the payoffs of the focal game constitute a small part of the player’s total fitness, selection is considered weak; if they constitute a large part, selection is
strong. Consider a generalized single-bout 2 x 2 discrete contest with the normal form matrix shown in Figure 6:

![Figure 6: Generalized payoff matrix for symmetric discrete contest with 2 alternative strategies.](image)

If the population size is very small and stable, strategy A will most likely take over the population if \( b > c \). If the population is stable but large, and selection due to the game is weak, A will most likely take over the population if \( a + 2b > c + 2d \). Suppose A is the TFT strategy and B is the AllD strategy when computed across an infinite number of successive interactions. We were earlier able to identify appropriate values of the payoffs and a probability of repeated interactions that caused this to be a give game (e.g., \( a > c \) and \( d > b \)). As discussed in Web Topic 10.5, any give game will have a mixture consisting of a fraction \( f \) of A players and a fraction \((1-f)\) of B players at which playing either strategy A or B gives the same payoff. We called this equilibrium frequency of A \( f_e \); it depended only on the relative payoff values in the matrix. Combining the computation for \( f_e \) with the condition in finite stochastic populations that makes TFT more likely to take over the finite population, \( a + 2b > c + 2d \), and letting \( f \) be the fraction of cooperators in the population, it can be shown that TFT is more likely to take over the population than AllD if \( f_e < 1/3 \). This is known as the “one-third law” and reflects the relative basins of attraction of the two possible outcomes in finite and well-mixed populations (Nowak et al. 2004). Unlike the infinite population case, rare TFT mutants can invade a finite population of AllD strategists and drive the population all the way to a population entirely of TFT players. Limiting population size can thus make cooperation the more likely ESS without having to invoke reputation, punishment, or other additional policies.

- **Large finite populations with sparse linkage:** Here we assume that each individual has interaction connections with only a subset of the entire population; however, the network consists of one large component and not of relatively independent groups. The effects of this type of spatial structure are usually studied under the rubric of evolutionary graph theory. The simplest cases involve viscous population in which both offspring dispersal and availability of cooperative partners tends to be limited to the immediate neighborhood of a focal animal. The relative roles of fecundity and survival in promoting or hindering the evolution of cooperation in viscous populations are summarized in Chapter 15; readers can seek additional details in Nowak and May 1992; Nowak 2006a; Nowak et al. 2010. The basic gist is that given the right demographic schedules, a pure cooperation ESS is much more likely to arise in viscous populations than in well-mixed ones. Interestingly, viscosity is not the only way that structure favoring the cooperation ESS might be achieved: if animals can preferentially select and modify links in their interaction networks, even when chosen partners are not immediate neighbors, cooperation can again become the more favored ESS (Ohtsuki et al. 2006; Pacheco et al. 2006; Fletcher and Doebeli 2009; Cao et al. 2011; Zhang et al. 2011).

Several authors have re-examined some of the classical games described above but with all players linked in a lattice. Given sufficiently favorable parameters, pure cooperation can spread until it fills the entire lattice, irrespective of whether the payoff matrix is for the Prisoner’s Dilemma or the Snowdrift game. However, under less favorable conditions, a population playing the Prisoner’s Dilemma game evolves into many clusters of pure cooperators that gradually increase in size, whereas Snowdrift economics cause cooperators and defectors to be such frequent neighbors that cooperation is not globally favored (Hauert and Doebeli 2004; Fu et al. 2010). In
another set of simulations, a public goods game with punishment was allowed to evolve on a lattice. Local feedbacks created a runaway process in which increased cooperation led to increased and more severe punishment, and vice versa. The result is an extremely strong combination of cooperation and punishment (Nakamaru and Dieckmann 2009).

- **Finite populations divided into many groups**: Dividing a population into relatively isolated groups can significantly change evolutionary outcomes. In one simple model by Killingback et al. (2006), the population is divided into many groups. Within each group, reproduction is a function of a public goods game whose productivity depends on the fractions of some maximal possible investment contributed by group members and the rate at which these investment are synergistically amplified. In each generation, a fixed fraction of offspring from each group is allowed to disperse and settle randomly among the existing groups. This generates variation in group sizes over time, and in the dispersion of individuals with different preferred levels of investment. There is no competition between groups, no punishment or rewards, no reputation effects, and no kin effects. At least for low but non-zero rates of offspring dispersal and synergistic amplification of two to three times investments, enough small groups whose members all have high rates of investment arise each generation to produce more offspring than are produced by the low investors in the population. The fraction of high investors thus increases over evolutionary time resulting in stable participation in the public goods game.

Several other models, again focusing on interactions within small groups, find that realistic parameters can lead to stable **generalized reciprocity**, in which a group member invests in any other group member if the investor’s most recent interaction resulted in it receiving an investment (Pfeiffer et al. 2005). This process can be enhanced if there is some physiological state that can track cumulative effects of recent interactions (Barta et al. 2011), partner choice is assortative rather than random (Rankin and Taborsky 2009), or social behaviors associated with exchanges are learned by copying group mates (Rutte and Pfeiffer 2009). A model by van Veelen et al. (2010) looks at the possible coevolution of group size and levels of cooperation and finds that only certain combinations of group size and cooperation are stable; this suggests that coevolution of group size and cooperation may be key to stable cooperative behaviors.

A final accounting in which division of a population into groups favors within-group cooperation is called **group selection**. As originally defined, the relevant models focused on the possibility that competition between groups can have fitness consequences that swamp out fitness effects due to competition within groups (Wilson 1975, 1990). However, high rates of offspring dispersal between groups can undermine this advantage (for similar reasons, the Killingback et al. model above only works for low rates of inter-group dispersal). The original discrete distinction between individual and group selection eventually evolved into quantitative accountings that partition selection into additive between-group and within-group effects (Wade 1985; Wilson 1997; Wilson and Dugatkin 1997; Kokko et al. 2001; Traulsen and Nowak 2006; O’Gorman et al. 2008; Wade et al. 2010). These are now called **multi-level selection** models. Other authors feel that this approach is simply an alternative accounting to the inclusive fitness method used widely for kin selection analyses (Gardner and Grafen 2009; Leigh 2010). Both accountings usually begin with the Price Equation, and as we discuss briefly in Chapter 9, the two approaches are often two ways to divide up the same pie. To be fair, most of the models we have reviewed in prior sections of this module do not even include competition between groups as a possible factor, whereas multi-level models include all possible factors. The question thus remains how often competition between groups contributes significantly to the overall fitness accountings once the within-group effects (e.g., those discussed in this module and those related to kin selection) have been accounted for. Further work will hopefully resolve this quantitative issue.

**Matching field data to theory**

Many examples of by-product mutualism and pseudo-reciprocity have been cited in the literature; we discuss some of these in a review of game theoretic models for environmental signaling in Web Topic 14.1. On the other hand, both direct and indirect reciprocity, policing, and market models have proved to be less easily assigned to specific biological examples. In part, this is because none of the alternative accountings listed above, this time including kin
selection and greenbeard biases, need to be exclusive determinants of a given example of cooperative behavior. On the contrary, mixes of economics are likely the rule rather than the exception. For that reason, and because different authors cannot often agree on which accounting predominates for a given phenomenon, we do not provide a list of examples assigned to each accounting here. Instead, the reader is directed to several published reviews that attempt to make assignments including mixtures of accountings to examples of animal cooperation. General reviews include Dugatkin (1998, 2002), Sachs et al. (2004), Silk (2007), West et al. (2007a), Bshary and Bergmüller (2008), Clutton-Brock (2009), and Connor (2010). Melis et al. (2010) compare the mechanisms and accountings that justify cooperation in animals with those in humans.

Further reading

A number of authors have proposed taxonomies or classification trees for the economics of cooperation among unrelated animals. Stark (2010) combines all the classical 2 x 2 models into a common framework, with a particular focus on cases where partial cooperation may evolve in both single-shot and iterated contexts. More details on the tree shown in Figure 1 can be found in Connor (1995), Leimar and Connor (2003), Bergmüller et al. (2007), Connor (2007), Bshary and Bergmüller (2008), Connor (2010), and Bshary and Bronstein (2011). Nowak (2006b) adds spatial pattern effects to the list (but leaves out some of the other accountings). His introduction to spatial and finite game models (Nowak 2006a) is an excellent starting point. Nowak and Sigmund (2005) provide a thoughtful review of indirect reciprocity and its relationship to alternative accountings. Reviews of cooperation economics that compare direct benefit economics with kin selection are provided by Queller (1985), Sachs et al. (2004), Lehmann and Keller (2006), Queller and Strassmann (2006), West et al. (2007a), and Clutton-Brock (2009). Bowles and Hammerstein (2003) provide interesting contrasts in the application of market theory to human versus animal social contexts.

Given that cooperation is often at most a two-ESS give game, it should not be surprising to find that some mutualisms in the past have now degenerated into pure defect states. Sachs and Simms (2006) use molecular techniques to identify examples in which mutualism is now absent, but was likely present in the past. Sanfey et al. (2003) discuss which parts of human brains are involved in selected cooperation games, and Soares et al. (2010) provide similar perspectives on the neuroendocrine bases of cooperative behaviors.

Several recent books try to tie much of this together. The first chapter of Karl Sigmund’s *The Calculus of Selfishness* (2010) provides a good overview; the rest of the book relies very heavily on complex mathematics. Nowak and Highfield’s *SuperCooperators* (2011) is also readable, but somewhat polemical and not always even-handed.

Literature cited


Web Topic 13.2 Examples of Social Integration Signals

Introduction

Social integration signals include a wide range of visual, acoustic, chemical, and tactile signals. Some of the signals are complex and variable in structure so that they can encode individual identity, an important requirement for group-living species with repeated interactions among group members. These signals also serve specific functions, such as synchronizing parental care behaviors in biparental species, facilitating parent and offspring communication, and coordinating group movements. In this Web Topics unit we provide rich media examples of identity signals, pair integration signals, parent–offspring signals, and group integration signals, following the outline in the main text.

Identity signals

Three examples of visual identity signals were illustrated in Figure 13.5. There are of course many more examples of patterns and colors that have evolved to be especially variable between individuals to encode individual distinctiveness. The interested reader should see the article on this topic by Tibbetts and Dale (2007). Individual chemical signals, or signature odors, can only be illustrated with gas chromatograph tracings showing the different components and proportions of these multi-chemical blends (see Clapperton and 1988; Buesching et al. 2002; Smith 2006). Similarly, electric fish also show very slight but meaningful individual differences in electric organ discharge waveforms (McGregor and Westby 1992). Here we focus on acoustic signature signals for a few social species in which individual identity is important. We show the spectrograms of calls from several different individuals. Click on the species name to see an audio–visual movie of the call series.

- **Jungle crow** (*Corvus macrorhynchos*) “ka” contact calls; individual identity is encoded in fundamental frequency, dominant frequency, FM shape, and duration (Kondo et al. 2010). (Audio files Courtesy of Noriko Kondo.)

- **Dhole** (*Cuon alpinus*) biphonic calls, containing a simultaneously given high-frequency *yap* and low-frequency *squeak*. Each component can also be given separately. The two-component call is given during peaceful group interactions and periods of group movement (Volodina et al. 2006). (Audio files courtesy of Elena Volodina.)
• **Bottlenose dolphin** (*Tursiops truncatus*) signature whistles; identity is encoded with a unique frequency modulation pattern that is learned or invented early in life and remains constant thereafter (see Sayigh et al. 2007; Sayigh and Janik 2010). (Audio files courtesy of Leala Sayigh.)

**Pair integration signals**

Here are some examples of pair integration signals in a variety of monogamous species, ranging from duets and other mutual displays to greeting ceremonies, courtship feeding, allopregening, and other tactile signals. Most of these examples are avian species. The majority of birds have a monogamous mating system, associated with pair bonds that last at least the duration of a breeding cycle and with biparental care of offspring. Pair bonds are maintained for
multiple years in sea birds, in which effective communication and coordination of parental activities are crucial for successful reproduction and improve as the pair gains breeding experience.

**Mutual displays**

- Greeting between mates in the closely related **crested penguin** (*Eudyptes pachyrhynchus*). This species is found in dense coastal forests along the New Zealand coast, in contrast to the rocky coastal and island habitat characteristic of its congeners: [http://www.arkive.org/fiordland-crested-penguin/eudyptes-pachyrhynchus/video-09c.html](http://www.arkive.org/fiordland-crested-penguin/eudyptes-pachyrhynchus/video-09c.html)
- Courtship, nesting, and chick feeding in **Adélie penguins** (*Pygoscelis adeliae*). This species typically lays a two-egg clutch which is incubated for about 34 days by both parents. A stint of incubation lasts an average of 12 days while the other parent is away foraging: [http://www.arkive.org/adelie-penguin/pygoscelis-adeliae/video-09b.html](http://www.arkive.org/adelie-penguin/pygoscelis-adeliae/video-09b.html)
- Pair bonding in the **Northern royal albatross** (*Diomedea sanfordi*). This very long-lived seabird (up to 40 years) doesn’t begin to reproduce until 8 years of age, and then breeds every other year, producing a single-egg clutch that requires 80 days to incubate and 240 days to fledge: [http://www.arkive.org/northern-royal-albatross/diomedea-sanfordi/video-09c.html](http://www.arkive.org/northern-royal-albatross/diomedea-sanfordi/video-09c.html)
- Courtship display in **ostriches** (*Struthio camelus*). The male forms a bond with one female who performs the diurnal incubation. He also attracts additional females who lay eggs in the pair’s nest but do not contribute toward incubation. The male incubates at night. This video clip shows the wing waving used by both sexes during courtship and the female mating solicitation display: [http://www.arkive.org/ostrich/struthio-camelus/video-09a.html](http://www.arkive.org/ostrich/struthio-camelus/video-09a.html)
- Duetting in **Neotropical wrens** of the “*Thryothorus*” taxon; this website shows a variety of spectrograms with accompanying audio files from the article by Mann et al. (2009). Species vary in how precisely male and female components are timed. Some species are cooperative breeders with complex choruses in which the males all sing one part in unison while the females sing a second part in unison: [http://media.brill.nl/behaviour/146/1/](http://media.brill.nl/behaviour/146/1/)
- Duetting by a pair of **purple-crowned fairy-wrens** (*Malurus coronatus*). Most of the *Malurus* fairy-wrens are cooperative breeders with subordinate helpers of variable relatedness to the breeding pair. Duetting occurs primarily or solely between the breeding pair. Extra-pair paternity is high in most species, but is low in the purple-crowned fairy-wren. This has been attributed to strong fidelity by the female and constant mate guarding by the male, and not to duetting, male courtship feeding, or frequent copulation (Hall and Peters 2008, 2009): [http://www.cell.com/current-biology/supplemental/S0960-9822%2807%2901263-8](http://www.cell.com/current-biology/supplemental/S0960-9822%2807%2901263-8)
- The precision of duets by **magpie lark** (*Grallina cyanoleuca*) pairs increases with age and experience; more precise duets are more threatening territory defense signals. This website contains two audio files from the article by Hall and Magrath (2007), the first one represents a well-coordinated pair, the second one a poorly coordinated pair (download the supplementary document to see spectrograms of these sounds): [http://www.cell.com/current-biology/supplemental/S0960-9822%2807%2901263-8](http://www.cell.com/current-biology/supplemental/S0960-9822%2807%2901263-8)
Courtship feeding: a common behavior in many species during the period of pair bond formation and courtship, in which the female may give a begging display much like the juvenile begging display and the male then feeds her. This behavior is not only a male mate attraction and copulation solicitation signal, but it also provides additional nutrition to the egg-laying female.

- Courtship feeding in crested kingfishers (*Megaceryle lugubris*): [http://www.youtube.com/watch?v=WkHX9p7vWnA](http://www.youtube.com/watch?v=WkHX9p7vWnA)
- Courtship feeding in the blue-eared kingfisher (*Alcedo meninting*): [http://www.youtube.com/watch?v=jckngisq_cs](http://www.youtube.com/watch?v=jckngisq_cs)
- Male black robin (*Petroica traversi*) courtship feeding his mate: [http://www.youtube.com/watch?v=bZCOS7gYDQw](http://www.youtube.com/watch?v=bZCOS7gYDQw)
- Courtship feeding in the woodpigeon (*Columba palumbus*) as a prelude to copulation: [http://www.youtube.com/watch?v=DPsfly1ej_o](http://www.youtube.com/watch?v=DPsfly1ej_o)

Mammalian examples

- A pair of hoolock gibbons (*Hoolock hoolock*) duetting together; the male has the dark fur color, the female has the buffy color. The monogamous pair jointly defends a stable territory and males often carry the offspring: [http://www.arkive.org/western-hoolock-gibbon/hoolock-hoolock/video-13.html](http://www.arkive.org/western-hoolock-gibbon/hoolock-hoolock/video-13.html)
- Titi monkeys (*Callicebus* spp) mate monogamously for life and live in nuclear family groups, with the pair’s accumulating offspring. The male performs more parental care than the female, carrying the young and bringing it to the female only for suckling. They often rest side by side with tails entwined, a tactile group bonding signal: [http://pin.primate.wisc.edu/factsheets/image/466](http://pin.primate.wisc.edu/factsheets/image/466)  
  [http://www.youtube.com/watch?v=U5-MP8nZIsU](http://www.youtube.com/watch?v=U5-MP8nZIsU)  
  They also duet or chorus as a pair or family group: [http://macaulaylibrary.org/audio/flashPlayer.do?id=88995](http://macaulaylibrary.org/audio/flashPlayer.do?id=88995)
- Male California mouse (*Peromyscus californicus*) grooming his mate; this is one of the few rodent species that forms monogamous pair bonds:
Parent-offspring integration signals

Examples of offspring begging signals: Here we show the offspring begging signals in a variety of species, primarily avian. In some species, adults bring a single item that can be given only to one offspring in a brood at a time; often the largest or closest chick is fed. Competition among chicks can be strong in such species. In other species, the adults bring a large amount of food, either multiple items or a semi-digested bolus that can be given to several or all of the young during a single provisioning trip. Note how in these species the parent attempts to feed each offspring.

- **Single-item feeders**
  - *Starling chicks* (*Sturnus vulgaris*) begging and being fed; note that only one chick is fed at a time): [http://www.arkive.org/european-starling/sturnus-vulgaris/video-09b.html](http://www.arkive.org/european-starling/sturnus-vulgaris/video-09b.html)
  - A second clip of bee-eater chicks showing intense sibling aggression when chicks vary significantly in size. In cavity and burrow nests, parents always enter from the same side and larger chicks can position themselves on this side and gain a significant feeding advantage: [http://www.arkive.org/white-fronted-bee-eater/merops-bullockoides/video-17b.html](http://www.arkive.org/white-fronted-bee-eater/merops-bullockoides/video-17b.html)

- **Multiple-item and regurgitation feeders**
  - *Bullfinch* (*Pyrrhula pyrrhula*) feeding chicks; this species is a seed regurgitation feeder, note that all chicks receive some food): [http://www.arkive.org/bullfinch/pyrrhula-pyrrhula/video-09.html](http://www.arkive.org/bullfinch/pyrrhula-pyrrhula/video-09.html)
  - *Skylark* (*Alauda arvensis*) chicks begging and being fed. Multiple items are brought and several chicks are often fed in one trip, note the care taken by the parent to spread the food around: [http://www.arkive.org/skylark/alauda-arvensis/video-09.html](http://www.arkive.org/skylark/alauda-arvensis/video-09.html)
  - *Green-rumped parrotlets* (*Forpus passerinus*). Most parrots produce medium-sized clutches and begin incubation before all eggs have been laid, resulting in highly asynchronous hatching and large variation in nesting size. Parents make a special effort to inspect and feed all chicks, especially the smaller ones (Krebs 1999). This video clip was taken inside an artificial PVC tube nest occupied by a wild pair of birds: [http://www.vimeo.com/9117349](http://www.vimeo.com/9117349)
  - *Scarlet macaw* (*Ara macao*) feeding chicks. Note the absence of conspicuous begging in this case, possibly associated with the small clutch size, egalitarian provisioning, and low level of competition between the chicks: [http://www.arkive.org/scarlet-macaw/ara-macao/video-09a.html](http://www.arkive.org/scarlet-macaw/ara-macao/video-09a.html)
  - *Humboldt penguins* (*Spheniscus humboldti*). In many seabirds, parents forage for a long period at sea and store multiple food items in their crops; the chicks reach into the parent’s open mouth to grab the regurgitated semi-digested items: [http://www.arkive.org/humboldt-penguin/spheniscus-humboldti/video-09b.html](http://www.arkive.org/humboldt-penguin/spheniscus-humboldti/video-09b.html)

- **Gouldian finch chicks** (*Erythrura gouldiae*) have a striking visual display, with blue phosphorescent beads on the sides of the beak, to guide the provisioning adult in the dark covered nest: [http://www.arkive.org/gouldian-finch/erythrura-gouldiae/video-09b.html](http://www.arkive.org/gouldian-finch/erythrura-gouldiae/video-09b.html)

- **Coyote** (*Canis lantrans*) female arriving at the den, she greets the pups, they beg for regurgitated food by nuzzling her mouth, and the pups fight over the food: [http://www.arkive.org/coyote/canis-latrans/video-09c.html](http://www.arkive.org/coyote/canis-latrans/video-09c.html)

- **Burying beetles** (*Nicrophorus* spp) adult and larvae: [http://www.youtube.com/watch?v=yRarHKpOf_8&NR=1](http://www.youtube.com/watch?v=yRarHKpOf_8&NR=1) and [http://www.youtube.com/watch?v=httCgCeOpAQ](http://www.youtube.com/watch?v=httCgCeOpAQ)

### Parental directive signals


- **Emperor goose** (*Chen canagica*) calling and leading chicks: [http://www.arkive.org/emperor-goose/chen-canagica/video-09b.html](http://www.arkive.org/emperor-goose/chen-canagica/video-09b.html)

- **Parent American coots** (*Fulica americana*) leading their young chicks from the nest out to the pond. Note the bright red head coloring on the chicks, which has evolved as a consequence of parental preferences for feeding more ornamented chicks, and also assists parents in recognizing their own chicks in cases of conspecific brood parasitism (Lyon et al. 1994; Krebs and Putland 2004; Shizuka and Lyon 2010): [http://www.vimeo.com/994897](http://www.vimeo.com/994897)

- **Female impala** (*Aepyceros melampus*) calling out her young faun from the creche to suckle; the faun has learned to recognize its mother’s call: [http://www.arkive.org/impala/aepyceros-melampus/video-09c.html](http://www.arkive.org/impala/aepyceros-melampus/video-09c.html)

### Group integration signals

Here are some examples of group integration signals, divided into categories of appeasement signals and group coordination signals.

#### Appeasement signals


- **White throated capuchins** (*Cebus capucinus*) grooming, including rubbing leaves on fur: [http://www.arkive.org/white-throated-capuchin/cebus-capucinus/video-05a.html](http://www.arkive.org/white-throated-capuchin/cebus-capucinus/video-05a.html)

- **Mandrills** (*Mandrillus sphinx*) allogrooming; note that in most of these incidents of allogrooming dominant male receives grooming by a subordinate male or female: [http://www.arkive.org/mandrill/mandrillus-sphinx/video-05.html](http://www.arkive.org/mandrill/mandrillus-sphinx/video-05.html)


**Badgers**
(Meles meles) allogrooming:  
http://www.arkive.org/badger/meles-meles/video-05b.html

- Plains zebra (*Equus quagga*) allogrooming:  

- Aggressive and submissive behavior in wolves (*Canis lupus*), plus howling, a territorial and group integration signal:  
http://www.youtube.com/watch?v=T8AFMq-j3w8&feature=related

- Teeth chattering in the Barbary macaque (*Macaca sylvanus*) serves several different functions. It is a submissive signal given by subordinates toward more dominant individuals, it is used to de-escalate aggressive encounters, it signals affiliation and likelihood of positive social interaction or tolerance, and it is given by dominants as a reassurance gesture of non-aggression (Wiper and Semple 2007):  

- Social interactions in hamadryas baboons (*Papio hamadryas*) are focused around the dominant male, who aggressively chases off intruders and controls the females. Other troop members behave submissively around him, averting their gaze or presenting their bottoms. There is virtually no courtship by the male; estrous females present their bottoms to be inspected by the male and copulation ensues:  

### Group coordination signals

- Group aggregation in the Emperor penguin (*Aptenodytes forsteri*). All nearby individuals cluster and huddle in a tight pack to withstand adverse weather conditions. The first section of the video clip shows courtship and nesting behavior and an incubation exchange, and the ending section shows chick begging and provisioning. The two-voice contact call can be heard throughout the clip:  

- Meerkat (*Suricata suricatta*) playful and defensive behaviors, including sentry duty:  

- Group decision-making in macaque troops. This video shows how one individual gives a signal to move, and then looks to see how many other individuals agree (“vote”) to follow; a minimum number of group members must agree before the whole troop moves. The audio narrative is in French:  
http://www.youtube.com/watch?v=lCDTE9cVfJ4

- European starling swarms (*Sturnus vulgaris*). Excellent footage and explanation of swarm formation in this common species; coordination is based on cues, not signals, as explained in Chapter 15:  
http://www.youtube.com/watch?v=XH-groCeKbE

- Snow goose (*Chen caerulescens*) flock take-off; some of the preflight signals can be seen here, such as directional head orientation and walking:  
http://www.vimeo.com/16582104

- Dominance and leadership in horse herds. This insightful horse trainer explains the subtle group dynamics within a herd of mares:  
http://www.youtube.com/watch?v=tql546leL6Y&NR=1

- Another interesting clip on horse social signals, showing herd movement coordination, aggressive, and submissive signals in the wild horses of the Camargue in southern France:  
http://www.vimeo.com/20403005

- Group movement and coordination signals in spinner dolphin groups (*Stenella longirostris*). The first ten minutes provides excellent footage and explanation of various acoustic signals such as tail, head, back, and side slaps, spinning leaps, and echolocation signals:  
http://directoryofkauai.net/blog/hawaiian-wildlife-and-spinner-dolphins-3

- Honeybees. As discussed in Chapter 13, honeybees use several signals to coordinate the fissioning of a colony
The waggle dance is given by a successful forager upon returning to the hive and signals the angle and direction to the food source to other foragers. This well-narrated clip explains how the dance components encode this information: http://www.youtube.com/watch?v=4NtegAOQpSs

The shaking signal recruits more receiver bees to take the nectar from the incoming foragers. In this clip, the central bee moves around inside the hive and directs the shaking signal repeatedly toward different surrounding bees: http://www.youtube.com/watch?v=Nf89PR_R8so

The piping signal is given both by virgin queens to call out other queens for a fight to determine dominance, and by scout bees to activate the workers about an hour before departure to a new home. In this video clip, the queen has been constrained in a cage and several worker bees are giving the high-pitched piping signal to stimulate her to move with them (courtesy of Tom Seeley).

The buzz-run display is produced in the one to two minutes before swarm departure and signals that lift-off is imminent. In this video, the queen of a colony that is about to fission has again been confined in a cage, and several buzz-runners are attempting to stimulate her to join the cluster of potential swarmer bees. The buzz-runner approaches lethargic bees in a zig-zag run, makes contact with them, and spreads her wings and buzzes, while pushing them to join the swarm (courtesy of Tom Seeley): <<Link to buzz-running video in Bee folder>>

Literature cited


Web Topic 13.3
Cognitive Models of Mate Choice

Introduction

As discussed in Chapter 13, females often use different signals and cues to ascertain whether a candidate male mate is a conspecific versus whether this male is of higher or lower quality than other candidates. However, in the end, a female’s evaluations of these two questions get melded into a single decision: she accepts him as a mate or she rejects him. This is but one example of decision-making in which multiple criteria must be evaluated before a choice can be made. For example, consider a forager that encounters a new food find: it will likely scan the abundance of food items, the average item quality, the degree of predator risk in that site, and the likelihood of finding better alternative sites before deciding to eat there. Two individuals facing a potential escalation during a conflict may try to assess the other’s relative body size, the condition of its armaments, the results of prior contests with the same individual, the proximity of coalition members, etc. When the cues or signals being evaluated reflect the same specific property in the sender, they will be correlated and thus redundant. Here, we are interested in cues, signals, and signal components that are used in a single decision but are largely uncorrelated and not redundant; they provide different information. This means that they might provide discordant information and that generates a cognitive challenge: what is the optimal way for a receiver to make a decision when one source of information favors one choice whereas another source favors the opposite choice? Because the issue was raised in Chapter 13 for females that are choosing mates, and this is the context that has largely been examined theoretically, we shall focus below on models of mate choice with conflicting inputs. However, it should be noted that this is a more general cognitive issue that may arise in a variety of animal communication contexts.

Cognitive options

We are interested here in multiple and uncorrelated sources of information about candidate males that a female might assess before deeming the male acceptable or not. These sources will likely include some mix of different male cues, signals, and components in multivariate signals. While several recent models focus on the different components in multivariate signals (e.g., dominant frequency and pulse rate versus call rate in anurans as indicators of species identity versus male quality), most of the models could handle any combination of the different possible sources. Before examining any of these models in detail, it is useful to list the various ways that a female might combine the uncorrelated information from multiple sources before making a decision (Jennions and Petrie 1997; Fawcett and Johnstone 2003; Castellano and Cermelli 2006; Phelps et al. 2006; Castellano 2010):

- **Single-source protocols**: Here, the female relies on information from only one of the sources and invokes only one criterion to make a decision (e.g., species identity); she is indifferent to information from the other source (e.g., once accepted as members of the correct species, males are chosen by chance). Most models assume females invoke a threshold for values of the favored source below which a male is rejected and above which he is accepted.

- **Amalgamated-source protocols**: In this case, observed values of each source’s data are transformed into some common currency and the transformed values from all sources are combined into a single composite score. There are several ways the transformed measures might be combined:
  - **Additively**: The simple algebraic sum of the transformed variables could be used, perhaps weighting each before addition according to relative impacts on fitness. Note that such a sum could be large even if one of the variables had a low value.
  - **Multiplicatively**: The score for a particular candidate male would here equal the product of the transformed values of the source variables. The product would be minimal if any variable were small in value, and maximal when all were large. Note that if stimuli are perceived by females on a logarithmic scale (e.g., Weber’s Law, [Web Topic 8.6](#)), the same relative scoring could be obtained by adding the logarithms of
the perceived stimuli.

- **Bayesian updating**: The conditional probabilities that a male was suitable given knowledge of a code and the female’s assessment of its values from each source could be entered separately into Bayes’ equation sequentially (in any order) to generate an updated probability that the male was suitable and then compared to some threshold value (Luttbeg 1996, 2002; Cheng et al. 2007). Unlike additive models, the magnitude of the change in a score after Bayesian updating depends on the value of the score before combining the new information.

- **Separate multiple-source protocols**: Here, the female would assess each source separately. Resolution of contrary outcomes would be resolved by assigning a priority order to the sources: only if a candidate male passed the highest priority criterion would he then be evaluated by the next criterion. There are two likely versions of this approach:
  - **Either**: The female accepts the male if the values of either source trait meet their respective criterion. This usually means assessing one trait first, and if the male passes the criterion, he is selected. If he fails that first criterion, the female then examines the second source and only accepts him if he passes the second criterion.
  - **Both**: In this protocol, the female examines the first trait and then goes on to assess the second trait only if the male passes the first criterion. A male must pass both criteria to be accepted. This is often called a hierarchical protocol. Note that this approach might generate outcomes that superficially look very like an additive model in which one criterion was much more highly weighted than the other before combination.

### Some relevant models

Early models of female mate choice tended to assume that: a) choice outcomes were binary (given male trait A then all females would always make the decision B), and b) females made no errors in assessing male attributes. While these related assumptions simplified the models, they are likely to be unrealistic. More recent work assumes that females make errors and thus that the outcome of any female decision will be stochastic. Outcomes are then best characterized along a continuous scale instead of a discrete one. Below, we examine several models that focus on female choice with these latter assumptions:

- **Fawcett and Johnstone (2003)**
  This model focuses on the tradeoff between the costs of female evaluation of male traits and the degree of error likely when assessing any given trait. It is an optimality model that seeks to identify the optimal protocol given a particular cost–error combination:

  - **Basic Assumptions**:
    - Males occur in two classes: suitable and not suitable. They display two traits that can take either of two states: if they are suitable, both traits exhibit the favorable state; if the male is unsuitable, both traits exhibit an unfavorable state.
    - Females are assumed to make errors in evaluating the state of each trait; the probability that a female errs by perceiving a favorable state in one of the traits of an unsuitable male (a false alarm) is assumed to equal that if she errs by perceiving an unfavorable state in a suitable male (miss).
    - Females pay a cost to search and find a male, and when they find one, then pay an additional but smaller cost for each trait that they take time to assess. If they find and accept a suitable male, they get a fitness benefit that must then be reduced by the costs spent in search and assessment. Females continue sampling males until they find one that is deemed suitable.
    - Alternative protocols considered in order of increasing “choosiness”:
      - **Anyone**: make no assessments and mate first male encountered
      - **Either**: assess favored trait first; accept if male appears to meet criterion; if not, examine second
and accept if male appears to meet criterion

—Single Trait: assess favored trait and accept male only if it appears to meet criterion

—Hierarchical: assess favored trait first and if male meets criterion, then assess second trait. Accept only if it meets both criteria in that order.

- **Outcomes and interpretations:**
  - When assessment costs and accuracies of assessment are the same for two traits, optimal protocol is for maximal choosiness (**hierarchical**) when costs of finding new males is low and accuracies are high; as either assessment error or cost of finding new males increases, optimum shifts to each successive level of choosiness eventually arriving at the **anyone** protocol. **Anyone** is also favored if suitable males become much rarer than unsuitable ones.
  - When costs of finding males are low to moderate, and assessment costs are equal but one trait is much more accurate than the other, the optimal protocols are **hierarchical** for intermediate accuracy combinations and **single trait** for more extreme ones. In each case, the favored trait is the one with the higher accuracy. As males become more rare, **single trait** becomes the dominant protocol over a wide range of accuracy combinations. At intermediate costs of finding males, **either** protocols replace **hierarchical** protocols for intermediate accuracy combinations. Interestingly, when males are rare, **hierarchical** protocols favor assessing the most accurate trait first whereas **either** protocols favor assessing the least accurate trait first; when males are common, the exact opposite orders are found for the two protocols. At very high costs of finding males, **anyone** is again the optimal protocol.
  - When costs of assessing traits are unequal, it is generally optimal for a female to begin by assessing the cheaper trait first.

- **Summary:** Whether it is better for a female to assess none, one, or two uncorrelated male traits, and if two, in which order, both vary with the costs of finding additional males, costs of assessing each trait, the accuracies with which each trait can be assessed, and the relative abundances of suitable and unsuitable males.

- **Phelps et al. (2006)** These authors ignore the costs experienced by choosing females and analyzed in the Fawcett and Johnstone (2003) paper. Instead, they investigate whether an amalgamated protocol can explain the frequently seen emphases on different male traits for recognition and discrimination studies of female choice. Many authors have cited such data as support for hierarchical protocols. Phelps et al. instead show that amalgamated protocols can produce very similar outcomes to the data cited in support of hierarchical protocols. Based on their model, they then examine data specifically designed to discriminate between the two protocols:
  - **Basic Assumptions:**
    - Females are assumed to combine information from uncorrelated male traits into a single preference score. How this is done is not examined.
    - Females use these assigned scores to both evaluate whether a given male has a score above a fixed threshold (e.g., species recognition) and compare two males who are both above threshold to identify the one with the higher score for mating (e.g., mate discrimination). A female encountering two males can either pick one for mating (as in forced choice experiments) or reject both (as can occur in free choice experiments).
    - Females make errors in assessment and the probability of assigning a given preference score value to a particular male is assumed to be distributed as a normal (bell-shaped) distribution with the mode equal to errorless judgments.
    - As in a signal detection model, females impose a threshold cutoff score below which no male is
accepted. The probability that a female will accept a given male is the total area under the normal curve for that male above the threshold cutoff. As the mode of the curve assigned to a male is increased, both the area under the curve and the probability he will be accepted for mating will increase. The function that describes how this probability increases with male mode will be nonlinear, as it depends on the shape of the function describing female error (in this case, a normal distribution). This aspect of the model is seen as the recognition process.

- The joint probability that a female will assign a given score to one male and another given score to a second male follows directly from the corresponding normal curves assigned to each male. The result can be graphed with the assigned value to one male on one axis, the assigned value to the other male on an orthogonal axis, and the joint probability of this combination on a third orthogonal axis. The volume under the resulting surface can be partitioned into those combinations of assigned male scores that lead to acceptance of one male by the female, those that lead her to accept the other male, and those that cause her to reject both. These volumes correspond to the overall probabilities that each of those outcomes will occur given the modal values for each male and the patterns of female error. These probabilities, which describe the discrimination process, are also nonlinear functions of male mode values. As noted by the authors, the discrimination function for a given male includes the special case for his recognition function when the modal value for a second male is very low relative to that of the first. That is, both recognition and discrimination tasks can be accommodated within a single continuous discrimination function.

- **Outcomes and interpretations:**
  - The authors argue that an apparent better fit of experimental data to hierarchical than to amalgamated protocols can be an artifact of performing forced choices that do not allow females to reject both males.
  - A second reason why hierarchical protocols have seemed to fit data better than amalgamated protocols is that the power of the tests applied by females varies depending on the how close the evaluated male’s scores are to the recognition threshold. Recognition tests (comparing a single male’s score to a threshold value) are statistically more powerful than discrimination tests when tested male scores are close to the female’s recognition threshold. Similarly, discrimination tests (comparing two male’s scores to see which is larger) are statistically more powerful when males are far above a female’s threshold. This difference in statistical power can give the impression that the recognition and discrimination processes are hierarchical and separate when in fact, they need not be: an amalgamated protocol would give a similar result.
  - The authors then identify several tests that are designed specifically to generate different outcomes for amalgamated and hierarchical protocols. These both show strong evidence in favor of amalgamated protocols. These tests and their outcomes are reviewed in more detail in Chapter 13.

- **Summary:** A simple model incorporating female error and assuming an amalgamated female protocol is both capable of explaining apparent emphases from animal experiments on some traits for recognition and some for discrimination, and provides a better fit to data obtained in experiments specifically designed to generate different outcomes for different protocols.

- **Castellano and Cermelli (2006)**
  In this model, the authors assume that female choice always begins with a recognition step. If a discrimination step is involved, it is assumed to occur after the recognition process. In this sense, they assume a hierarchical ordering of steps. They then consider several different protocols for how females might implement a discrimination step.

  - **Basic Assumptions:**
    - Male advertisement signals are allowed to vary along multiple uncorrelated dimensions.
    - Females collapse the multiple-dimensioned male signals into a one-dimensional scale of recognition scores. The score for each male is then compared to a threshold value and males with less than
threshold values are rejected as unsuitable. Because females can err in assigning these scores, the outcome in this step is treated as a probability of accepting a male.

- If two males are deemed acceptable, the female then applies a second discrimination step to choose between them. This step might use the same score created for the recognition step, or it might require the assignment of a different set of scores based on the same signals.

- The model focuses on computing the probability that a focal male will be chosen as a mate when it and a competitor are both encountered by a female. There are two possibilities: a) the focal male is found acceptable during the recognition step but the other male is not; or b) both males are found acceptable and the female must then apply a separate discrimination function to select between them. The probability that a will occur is the product of the probability that the focal male is accepted during the recognition step, and the probability that the other male is rejected. The probability that b will occur is the product of the probabilities that each male will be found acceptable during recognition. The net probability for b is then this product times the probability that the focal male will be chosen during a discrimination comparison. The net probability that the focal male will be chosen is then the probability from a plus that for b (since this is an “OR” situation).

- Selection on the recognition function is assumed to be stabilizing (e.g., there is an optimal male trait value and males that are increasingly different from this optimal form are increasingly likely to be rejected. Selection on the discrimination function, if one is applied, is assumed to be directional: the more extreme a focal male’s signal in one direction, the more likely he is to be selected.

- The authors then examine an example in which each male’s signal has two uncorrelated components: one is more useful for recognition, and the other is more useful for discrimination. They examine two ways females might use these two components: a) multiplicatively amalgamating transformed values of each component’s values into a single composite score; or b) keeping the transformed values of each component separate and using them in different steps.

- They then consider three protocols:

  — **One step amalgamated protocol**: In this case, females use the amalgamated score for the recognition step, but do not bother with a discrimination step: if two males are both acceptable, one of them is chosen by chance. There is thus no discrimination function needed.

  — **Two step amalgamated protocol**: Females use the same amalgamated score for both a recognition step and a discrimination step. This is similar to the Phelps et al. model above.

  — **Two step separated protocol**: Females use the score extracted from the first component for the recognition step, and that extracted from the second component for a discrimination step. This is a classical hierarchical model in which only males that pass the first recognition filter are then considered for a discrimination contrast.

- **Outcomes and interpretations**: By varying parameter values in simulations, the authors found that:

  - Holding the directional selection component fixed, both two-step protocols provided a female with much more accurate recognition performance than did the one-step protocol.

  - Holding the recognition selection fixed, the two-step separated protocol provided the most accurate discrimination between males, followed closely by the two-step amalgamated protocol; the one-step protocol, not surprisingly, provides only weak discrimination between males.

  - In both two-step protocols, the degree of choosiness in the recognition step could be used to fine-tune the accuracy of the discrimination step; however, fine-tuning of the amalgamated two-step can be done in a way that does not decrease recognition accuracy whereas this is not true for the separated two-step protocol.
Summary: This model confirms the Phelps et al. conclusion that the same amalgamated scores of multivariate male signals with uncorrelated components can be used for both recognition and discrimination with high accuracy. Hierarchical models are only marginally more accurate, and may impose costs in other performance measures. As with both prior models, having access to multiple uncorrelated signal components can improve the accuracy of female choice.

  In these papers, the authors compare the outcomes of female choice using additive amalgamation versus multiplicative amalgamation protocols. Note also that none of the prior models allow for refinement of female assessments due to cumulative sampling, even in the Fawcett and Johnstone model where females sample males successively until one meets the suitability criterion. As we discuss in Chapter 8, cumulative sampling is a common strategy that can improve the accuracy of decision makers. Here, the authors examine the two amalgamation protocols in a random-walk model in which females are able to sample repeatedly before making a choice.

  - Basic Assumptions:
    - Multivariate male advertisement signals contain two uncorrelated components: C1 is most useful for recognition, whereas C2 tends to be more useful for discrimination.
    - Females assign a single-dimensional attractiveness score to each male by transforming each signal component’s value into a common “attractiveness” currency and then amalgamating the perceived attractiveness values for the two components. They can amalgamate transformed components additively or multiplicatively.
    - In a recognition task, successive sampling of the same male is assumed to generate a running sum of its attractiveness score values. The recognition step ends when a female accepts a male as suitable because his running sum exceeded some threshold, or rejects the male because some set maximum number of samplings is exceeded.
    - In a discrimination task, the differences between the perceived attractiveness scores of two males given successive samplings are added cumulatively (using the same individual’s score as the subtracted term). Sampling stops when the absolute value of this sum exceeds some threshold value: if that final sum is negative, the subtracted individual is chosen; if the sum is positive, the other male is chosen. The probability that any given male will be selected is a sigmoid function of the threshold value and the average difference between its score and that of the other male.

  - Outcomes and interpretations:
    - Because the recognition signal component is under stabilizing selection, two males that are both dubbed suitable will have similar values for C1. This means that C1 will contribute little to the difference between two males’ scores used in a discrimination step if amalgamation is additive. **Additive amalgamation** causes discrimination to depend mostly on the differences in the males’ values of their C2 component.
    - When **multiplicative amalgamation** is the basis of score computation, the running sum of differences between male signals depends on the values of both C1 and C2. Depending upon the error level with which females assess C2, the strength of the discrimination preference for one male over the other can increase continuously as the average values of C1 for the two males increases, or even peak at some intermediate value of C1. The C1 component can thus amplify the differences between males in the C2 component during female discriminations.
    - This predicts that if amalgamation is additive, the strength of female discrimination between males should be dominated by C2 values and be relatively independent of C1; if amalgamation is multiplicative, changing C1 values should change the strength of discrimination for any given difference in C2 values between the males. The author then presents experimental data on an Italian frog that supports the multiplicative amalgamation protocol.
Summary: This publication extends both the theory and the data in support of amalgamation over separated and hierarchical protocols in female choice of mates using uncorrelated multivariate signal components, and provides evidence that multiplicative amalgamation is the more likely process.

Perspectives

The examined models have provided a good start in understanding the optimal strategies for females choosing males, and more generally, deciders incorporating multiple sources of information into a single decision. Comparisons between these models and data support female choice protocols that amalgamate information from different sources into a single score before undertaking recognition and discrimination tasks. However, there are still many questions that have yet to be examined. While relative costs of finding mates and assessing them formed the focus of the Fawcett and Johnstone (2003) models, costs were not considered by any of the other models considered here. Combining costs with alternative protocols might be of value; an initial step in this direction can be found in a recent model by Castellano and Cermelli (2011). Although both Phelps et al. (2006) and Castellano and Cermelli (2010) mention possible Bayesian updating, this protocol for combining information across multiple sources and over time has yet to be formulated in a way that can be compared to the other protocols described here (but see Luttbeg 2002). A common focus in the models reviewed here is on multiple and uncorrelated sources of information; redundant multivariate signals were excluded from consideration. There are good reasons to believe that optimal multivariate signals have components that are partially but incompletely correlated (Ay et al. 2007). Examples that seem to fit this circumstance include the color intensity and size of genital swellings in receptive female baboons (Higham et al. 2008), and the individual compounds in complex pheromonal mixtures of lizards that indicate different but not always uncorrelated aspects of overall health (Lopez et al. 2006). A more general model than those considered here might vary the degree to which multiple information sources provide correlated information.

Further reading and examples

Each of the Phelps et al. and Castellano and Cermelli papers compares their models to their own favorite anuran species. Clearly, one would like additional contrasts on these species, and broader contrasts across other species. Among other experiments on anurans, Baugh et al. (2008) show that as many as seven continuously-varying components in male calls are combined by females into their threshold recognition tasks. Schul and Bush (2002) find that two closely related tree frog species both perform recognition tasks based on pulse duration and inter-pulse interval in male calls: in one species, these are amalgamated additively, and in the other they are amalgamated multiplicatively. Burke and Murphy (2007) show that females in another species of the same genus of tree frogs amalgamate male call rate and call duration data multiplicatively before accepting or rejecting mates.

Several studies have identified tradeoffs in the relative weighting of recognition criteria and discrimination criteria during mate choice. For example, crickets appear to emphasize recognition criteria over discrimination traits (Scheuber et al. 2004). Spadefoot toads also stress recognition tasks over discrimination tasks where populations historically overlap with related species, but may not if heterospecific overlap is uncommon (Pfennig 2000). Novel or rare hybrid Drosophila may be preferred over conspecifics if they carry a sufficiently favored discrimination trait; here the discrimination step can overrule the recognition one (Boake et al. 1997). In guppies and sticklebacks, the size and intensity of male colored areas and the rates of display can all affect female choices but with different weightings depending on contexts (Kodric-Brown and Nicoletto 2001; Kunzler and Bakker 2001; Karino and Urano 2008; Karino et al. 2010). Other examples are reviewed in Chapter 13.

Some additional theoretical treatments provide further insights. Candolin (2003) provides a broad review of why multiple criteria might be favored in female choice. The issues of costs and how these might affect optimal female decision protocols have been examined by several authors. Chittka et al. (2009) focus on the general problem of speed versus accuracy in decision-making, Bateson and Healy (2005) conclude that assessment costs and time pressures are likely to favor heuristic decisions by females and multiple criteria may facilitate these heuristics. Wiegmann and Angeloni (2007) examine the role of female search and assessment costs in setting suitability thresholds when not all fitness-
determining traits in males are assessable by females. While they focus on a single male trait, they point out that the outcomes will be similar if multiple traits are combined during female assessment into a single amalgamated score.

**Literature cited**


Karino, K. and Y. Urano. 2008. The relative importance of orange spot coloration and total length of males in female


An Overview of Begging Models

The bigger game

The history of evolutionary game modeling of parental care strategies is unusually convoluted. Initially, researchers tended to focus on three separate games as if they were independent. The first involved conflict between the parents as to which one, if either, should do any parental care (Dawkins and Carlisle 1976; Maynard Smith 1977; Grafen and Sibly 1978). This initially was called the “desertion game” where the discrete alternative strategies for either parent were to fully commit to or do no parental care; later models were continuous games in which each parent could contribute a level of parental investment from a wide and continuous range. The second game recognized that high parental investment in any one brood would likely decrease a parent’s remaining lifetime resources for later broods. Since offspring in any given brood favored high parental investments, whereas parents were likely to be selected to hold back, the result was a parent–offspring conflict game (Trivers 1974; Macnair and Parker 1978; Parker and Macnair 1978, 1979). This was treated as a sequential game for the parents and ESSs were optimal policies by which a parent should distribute its resources over successive broods. Finally, offspring within the same brood are likely to compete with each other for whatever food and parental care was available (Macnair and Parker 1979; Harper 1986; Parker et al. 1989). The degree of kin relatedness among nestlings may set a limit on how selfish any one offspring should be (Hamilton 1964).

It soon became clear that these games were not independent, and strategic decisions by any one player in one game could significantly affect the options and payoffs of the same or other players in one of the other games. The earlier analyses are best thought of as sub-games within a much larger game. As reviewed by Parker et al. (2002b), the simplest global game is a two-role asymmetric scramble with more than one player in each role (e.g., an N-person game). The two asymmetric roles are parent and offspring. The game is an N-person scramble (instead of a dyadic contest) because the payoffs within a single interaction to a player in one role depend both on the relative abundances of alternative strategies in its own role as well as the relative abundances of alternative strategies in the other role. The sequential aspects of the parent–offspring conflict game are usually simplified by finding a single optimal policy that applies to all successive broods over a lifetime. The overall game can be diagrammed as in Figure 1:

![Figure 1. Network of interactions defining larger parent–offspring conflict game.](image-url)
When there are asymmetric sub-types within either or both of the parent and offspring roles, the game is even more complicated. For example, asynchronous hatching can result in nestlings of different body sizes and thus different competitive abilities when begging. If one sex is more likely to defect and leave parenting to the other, this generates an additional asymmetry.

There are so many conflicts in this game that the combined “battleground” is large (Godfray 1995a). These conflicts arise because the allocation of parental care that would maximize fitness for one party is invariably an allocation that is suboptimal for other parties. As with many evolutionary game models, the resulting ESSs are usually nobody’s optimal outcome; instead, ESS equilibria occur where each type of player’s current strategy is the best response to the best responses of all of the other types. At an ESS, each type of player will have its own best response: for offspring, that is a level of begging directed toward each type of parent, and for the parents, it is the amount of parental care (including feeding) provided to each type of offspring. An ESS will thus specify the best response for each of the types in the game.

There may be more than one ESS in a game this complex. In addition, these ESSs may be swayed toward or away from any given player type’s optimum as contexts change. If the optimum is an intermediate value, an ESS that pushes a party’s best response to either a lower or higher value will decrease its fitness below the maximum possible and thus be suboptimal. The ways in which the ESSs shift have been examined theoretically for the following contextual contrasts:

- One parent (usually male) deserts leaving the other to undertake all parental care versus both parents share in the raising of offspring
- Offspring are all closely related (same father and mother), only partially related (different fathers due to extra-pair copulations or different mothers due to egg dumping), or not at all related (nestling shares nest with offspring of nest parasite).
- Parent(s) are likely to produce many versus only a few broods per lifetime
- Parent(s) determine how much food will be provided to a given brood (supply determines demand) versus offspring begging determines amount of food a given brood receives (demand determines supply)
- Parent(s) control how much each offspring is fed versus offspring interactions determine the amount each offspring is fed
- Offspring compete with initial strong asymmetries (dominance effects) versus offspring initially have similar competitive abilities (resulting in so-called scramble competition)
- Offspring signal need honestly to parents versus do not signal

We shall take up some of these specific cases below.

**Some nuts and bolts of begging models**

There are several commonly invoked methods used to find ESSs in begging models. Nearly all analyses use a marginal value type of analysis to identify the optimal investment that should be spent in any one episode (whether foraging on a patch, defending an ephemeral resource from competitors, or investing in a particular brood). The optimal investment is the one that maximizes the realizable rate of benefits relative to costs (Parker 1974; Charnov 1976). On a plot of benefits versus costs, this can be drawn as a straight line with positive slope (Figure 2). Lines with increasing slopes but the same intercept represent lines with higher marginal benefits (i.e., a small increase in cost results in a higher increase in benefits). The problem is to find which line has the highest slope but is also realizable given the phenomenological relationship between benefits and costs. The latter is usually drawn on such a plot as an increasing
but asymptotic (or rapidly decelerating) function. The function may or may not have an initial minimal investment that is required before any benefits accrue: this is shown on the graph of the function as a straight line along the horizontal axis. The point on this phenomenological relationship that is just touched by one of the possible straight lines yields the optimal rate of benefit to cost that is feasible. If the animal uses this criterion for all successive episodes, it will maximize its net fitness.

Figure 2. Marginal value analysis of optimal strategy. (A) Beginning at some initial benefit level with no investment, benefits are assumed to increase linearly with costs. Blue dashed lines show three possible benefit/cost rates: higher marginal rates of benefit per unit cost produce lines with steeper slopes. (B) Phenomenological relationship between benefits and costs for some real situation. Initial function is flat because it requires some minimal initial investment before any benefits accrue. If the situation is foraging, the flat portion might represent the investment required to find a new food patch; if the situation is breeding, the investment might be building a nest; if the investment is parental provisioning, a minimal amount of food must be given to an offspring before it has any chance of surviving. (C) To find the optimal investment, given the phenomenological function, different possible rate lines are drawn on top of the phenomenological line. The high rate line never touches the phenomenological curve, so is not realizable. The low rate is realizable, but not the highest realizable rate. The middle line just touches the phenomenological curve and is thus the highest realizable rate. The corresponding investment (where vertical dotted line intercepts horizontal axis) is the optimal investment.

In begging models, it is assumed that fitness benefits (the vertical axis in the relevant marginal value plots) increase with increasing parental investment but with diminishing returns for both parents and offspring. Hence these models have decelerating phenomenological curves. The shape and height of the phenomenological curves can vary depending upon the various contexts listed earlier. In addition, both the slope and the intercept point for the possible benefit/cost lines can vary with contexts. For example, the slope of the lines will be less if only one parent instead of two cares for the young, but the intercept will be higher in single parent cases if this also creates a greater range of possible sibling relatedness values (Parker et al. 2002b). The task for a particular context is thus to identify the correct phenomenological curves and the correct rate lines.

These efforts only define the optimal amount of parental investment for each type of party in the bigger game. Where the optima for different types are different, there is conflict of interest over how large an investment parents should undertake. As noted earlier, the fitness payoff to any given role (parent or offspring) depends on what strategy it adopts, what strategies its fellow role members adopt, and what strategies are adopted by members of the other role. At an ESS, all members of any given role should adopt the same strategy. Thus at the ESS, the payoff for a member of a given role depends only on what strategy all of its members adopt, and what strategy all members of the opposite role adopt. At an ESS, selection does not favor either role changing its current strategy. Thus the first derivative of the continuous function describing lifetime fitness as a function of strategy value for a role will equal zero if all members of that role adopt the ESS strategy value. Since the first derivatives of the lifetime fitness functions for parents and offspring both contain terms representing their own and the other’s strategy values, and both equal zero at the ESS, there are two equations with two unknowns, so one can solve for the ESS strategy for the parents and the
corresponding strategy for the offspring. In many cases, this ESS pair of strategies will not sit on either role’s optimum as defined by the marginal value analysis. A graph of two optima and battleground region for the traditional parent–offspring conflict is illustrated in Figure 13.18 of the main text.

Other assumptions shared by most models include:

- Asymmetric game with continuous strategy sets: usually levels of begging for the offspring role and sensitivity to begging behaviors for the parent role.
- Parental investment in the current brood erodes parental resources available for future broods. The problem for the parent is undertaking the optimal number of breeding episodes, and then distributing their finite total available investment among them in an optimal way (see Chapter 9).
- Offspring fitness depends on the parental investment they receive directly, and that provided to siblings (both in the same brood and in their parents’ future broods) discounted by their relatedness to those siblings. Increasing one’s own share of the parental investment increases its own fitness but at the expense of the indirect fitness it might have received through its kin. The optimal balance depends on the shape of the functions relating offspring fitness to parental investments.
- To prevent begging from escalating to excessive levels, many models include an increasing cost for higher levels of begging. The cost may be an individually experienced cost such as higher energetic expenditure, or a cost shared by the whole brood, such as increased risk of attracting predators.

Below we describe several different parent–offspring conflict models, including the classical scramble competition and honest signaling models, tug-of-war models, quantitative genetics models, parental negotiation models, and a sibling negotiation model (see also Mock and Parker [1997] and Godfray and Johnstone [2000] for reviews of some of these models).

Parent–offspring scramble competition model (Parker and Macnair 1979)

Context:

Offspring compete for access to food brought by parent by giving conspicuous displays.

Synopsis:

- Siblings do not differ in competitive ability, but instead engage in scramble competition for parental attention. The offspring’s level of begging or jostling varies over a continuous range. The higher the level, the more food the individual receives relative to siblings.
- One parent provisions the offspring. The sensitivity of the parent to the offspring’s behavior varies over a continuous range from completely insensitive to highly sensitive. For any level of sensitivity greater than zero, the parent uses a matching rule, giving the offspring that behave more vigorously a larger amount of food relative to offspring behaving less vigorously. In other words, the parent passively feeds the offspring presenting the greatest stimulus.
- Begging is costly for the offspring, either energetically or by way of attracting predators, and therefore reduces offspring survival.
- The model assumes that offspring respond to higher levels of obtained resources by reducing the intensity of their begging or jostling behavior.
- Variants of the model consider monogamous or polygamous mating systems so that offspring are full or half sibs, respectively; one or two attending parents; and intra- or interbrood conflict. In the case of intrabrood conflict, the parent’s total investment for the whole breeding attempt is fixed, and an increase in feeding to one offspring in a brood reduces feeding to other offspring in the same brood. In the case of interbrood conflict, an increase in total parental investment for the current brood decreases parental survival or investment in future broods.
Conclusions:

- The optimal food intake rate for the offspring is greater than the optimal provisioning rate of the parent. This difference establishes the battleground for this subgame. The difference is greater when offspring are half sibs compared to full sibs, when there are two parents compared to one parent, and for intrabrood compared to interbrood conflict.

- At the resolution ESS, the parent provides more food than is optimal for it, but less food than the optimum preferred by the offspring, i.e., the solution is a compromise lying somewhere between the two optima.

- Because of the competition between offspring in the same brood, each individual offspring is selected to demand a greater share of the food brought to the brood than its sibs are selected to yield. Extravagant begging displays or sib–sib aggressive behaviors are expected to evolve to manipulate parents into bringing more food than they would prefer.

- The compromise ESS predicted by this model depends on there being a moderate cost to the offspring of begging or jostling. If begging is extremely costly, such that the fitness of an offspring that solicits without receiving a reward drops off steeply, begging vigor must remain at a minimally low level, and the ESS provisioning level can shift to either the parental optimum or the offspring optimum. The parent-wins ESS is more likely to occur when begging is energetically costly, when the parent pays little cost for being insensitive, and with intrabrood conflict. The offspring-wins ESS is more likely to occur with high shared begging costs (i.e., risk of predation) and with interbrood conflict. In this context, Zahavi (Zahavi 1977b; Zahavi and Zahavi 1997) proposed the blackmail hypothesis to explain the function of loud begging (i.e., the parent is obliged to feed the offspring to keep their begging at a low level). However, it is competition, not blackmail, that pushes offspring to beg more vigorously.

Related models:

- The three earlier articles in the Parker-Macnair series (Macnair and Parker 1978; Parker and Macnair 1978; Macnair and Parker 1979) establish the different parental and offspring optima for different mating systems and types of brood conflict (intra or inter), but do not compute the resolution ESS as in Parker and Macnair (1979). The fifth article in the series (Parker 1985) considers the resolution outcome when one versus two parents perform the provisioning, and finds that conflict is greater (offspring are more demanding) when two parents collaborate.

- Harper (1986) developed a parent–offspring coevolutionary model in which the offspring can vary its rate of begging and rate of change in begging intensity with changes in parental investment level, and the parent can vary its provisioning investment with changes in begging intensity. These were assumptions in the Parker-Macnair model, but are allowed to evolve in this model. At the ESS, offspring reduce their begging when parental investment is high, and parents increase their provisioning rate when offspring begging rate is high. This means that any fluctuations in parental investment are compensated for on subsequent feeding trips. Total begging intensity of the brood should increase with brood size, but in larger broods begging intensity per offspring is lower.

- Godfray and Parker (1992) also expanded the Parker and Macnair model to examine the role of brood size. Larger brood size results in increased sibling competition. Parents may be able to increase their fitness by reducing brood size, in order to reduce this cost of competition.

Asymmetric sibling competition (Parker et al. 1989)

Context:

Offspring differ in competitive abilities.

Background:
The Parker-Macnair models were expanded to examine what happens when offspring differ in competitive abilities. This model was stimulated by the frequent occurrence in birds of asynchronous hatching, caused by the parent starting incubation before all of the eggs have been laid. The result is variation in nestling age and size. Older nestlings often gain a significant advantage over their nestmates, and in many cases younger nestlings fail to receive sufficient nutrition and die, especially if food availability is low. The question addressed is: how selfish should stronger sibs be?

**Synopsis:**

- Parental investment in a given brood is fixed, and only one breeding event is considered, so this model is based on intrabrood conflict only. Two time scales are considered: the whole period of parental care for the brood, and the short-term period (one day or a single feeding event). Parental sensitivity does not evolve in this model, so it is strictly a sib–sib conflict subgame.
- Offspring differ in competitive ability, and allocation of food depends on the asymmetry in offspring behaviors. Two types of asymmetries are considered in separate models.
- In the hierarchical model, siblings form an age or size-based dominance hierarchy at no cost to the dominants. Dominants physically outcompete subordinates for the food. Two- and three-sibling broods were modeled separately. The alpha (A) sib has first access to food resources brought by the parent, and the beta (B) sib gets what is left over. With three siblings, the gamma (C) sib gets what is left over after A and B have taken what they want.
- In the scramble competition model, the two sibs differ in the benefits and costs of display. The begging rate for the siblings is allowed to evolve independently, and each sib chooses its optimal level of display. The parent feeds the sib with the more stimulating target.
- The ESS solution occurs at the point where the marginal gains of the two (or three) siblings are equal.

**Conclusions:**

- **Hierarchical model results:** When food resources are plentiful, the A sib gains little by denying the B sib access to food, so A and B receive nearly equal shares and their fitnesses are similar and close to the maximum attainable. As food resources become more scarce, more food is allocated to the A sib. In the short-term version, A may even allow B to obtain the larger share, if B’s marginal fitness gain is higher.
- **Scramble competition model results:** If there is no cost to begging, begging levels escalate indefinitely and there is no ESS. An increasing individual energetic cost for higher begging levels is therefore required. At the ESS, the A sib expends less energy on begging than the B sib, but A’s display is more effective. As the difference in competitive ability increases, B’s begging costs increase. If food resources are somewhat limited, B’s begging costs may peak at an intermediate level of asymmetry in competitive ability; at this point, B is begging more vigorously than A and receiving a larger share of food, but this benefit is balanced by its greater begging costs. At low food levels, sib A takes the greater share of the food because the B sib cannot afford to display more vigorously.

**Related models:**

- Rodriguez-Gironés et al. (2001) expanded on this model by allowing sibs to employ different forms of competitive strategies. Two offspring strategies are considered—signaling (begging) behavior and non-signaling (aggressive) behavior—which can vary in their weighting. The model also includes a co-evolving parental response and interbrood effects. Increases in begging intensity can cause the parent to increase its rate of provisioning, whereas increases in non-signaling behaviors do not increase provisioning rate but do affect allocation of food between the siblings. In the model with only signaling behavior, more competitive offspring beg less but obtain a greater share of the food. In the model with only non-signaling behavior, parents deliver a fixed amount of food and more competitive offspring obtain a greater share. When both types of offspring behaviors are allowed and combined additively, the result depends on the degree of asymmetry: for low asymmetry, both sibs invest in signaling, and for high asymmetry, the less competitive sib invests in signaling and the more
competitive sib invests in non-signaling behavior. When behaviors are combined multiplicatively, competitive sibs invest more in signaling. Under most scenarios, more competitive sibs receive a greater share of food. The authors conclude that signaling is costly and wasteful (e.g., if a weak sib begs vigorously to induce the parent to bring more food, the stronger sib will just take a greater share of it), so signaling is expected to play a minor role in determining the allocation of food.

Honest signaling model (Godfray 1991, 1995b)

Context:
Offspring transmit information about their need for food to the parent using begging vigor as a signal.

Background:
Begging as a signal of offspring need was a common idea previous to Trivers (1974), but was abandoned in the first series of parent offspring models by Parker and Macnair (described above) that emphasized sibling competition. These models suffered from the fact that they assumed fixed behaviors by parents and offspring—parents respond to increased offspring solicitation by providing more resources, and offspring respond to increased resources by decreasing their solicitation level. A better model would allow these responses to evolve (e.g., as in Harper 1986). The development of honest signaling models by Zahavi and Grafen (Zahavi 1975; Zahavi 1977a; Grafen 1990a, 1990b) revived the idea that begging behaviors could be considered honest signals of need, as long as they were costly. The honest signaling framework allows the investigator to seek the conditions under which begging behaviors can become honest indicators of offspring need.

Synopsis:
- Offspring vary in their condition, a state variable that determines their need for food. An offspring in poor condition gains a higher marginal benefit when it receives food from the parent than an offspring in good condition.
- The (single) parent is selected to give more resources to young in poorer condition. The parent cannot assess condition directly via cues, but must obtain this information from signals given by the offspring.
- Offspring fitness depends on condition, level of solicitation, and amount of food resources obtained from the parent. As in other models, offspring fitness increases monotonically but at a decelerating rate with increasing resources received. The condition (or need) component is included as a constant that determines the rate at which the fitness benefit curve (Figure 2) approaches the asymptote; greater need means that the fitness curve rises faster and is more concave. Solicitation is costly, so fitness decreases linearly with increasing solicitation level. Offspring also obtain indirect fitness benefits from any future offspring the parent raises, discounted by relatedness.
- Parental fitness depends on the number of total offspring raised. An increase in provisioning to the current brood increases the current offspring’s chances of surviving, but decreases the parent’s future reproductive rate.
- The amount of resource obtained by the offspring is some function of the level of display; this function is initially unknown and allowed to evolve.
- In Grafen (1991), there is a single offspring raised per year over a succession of years, so only interbrood conflict is considered.
- In Grafen (1995b), two offspring simultaneously compete for a fixed amount of food brought by the parent, so only intrabrood conflict occurs. The parent adjusts its distribution of food to the offspring until the marginal gains from allocating more food to each offspring are equal. Each offspring is also sensitive to the nestmate’s begging level.

Conclusions:
• There is an ESS pair of strategies in which the offspring signals at a rate that is determined by its condition and increases as its condition declines, and the parent allocates more resources to the offspring using the rate of display as an indicator of offspring condition.

• Offspring are constrained from exaggerating their need by the cost of begging and the loss in indirect fitness from future sibs.

• Honest signaling of need is locally stable as long as begging is costly and the value of obtaining more resources increases with diminishing returns. An offspring in maximum condition does not display at all, as it receives no benefit from doing so.

• The ESS resides at the parental optimum; as long as the parent receives honest information of offspring need from the signals, the parent controls food delivery at its optimal level.

• The extent of costly begging depends on the variance in the condition component of fitness. If condition varies very little within and between offspring, it is more difficult to achieve the honest signaling ESS.

• In the case with two young per brood, if the cost of solicitation differs between offspring with the same need, the offspring for whom solicitation is cheaper will misrepresent their needs and obtain more resources, which moves the ESS off the parental optimum. Furthermore, if one is deprived of food and begs more, the other one increases its begging rate slightly.

**Related models:**

• Rodríguez-Gironés et al. (1996, 1998) re-examined Godfray’s models and found that a second equilibrium exists in which young do not signal and the parent provisions according to a statistically probable distribution of offspring need states; fitness for both parties is higher at this ESS than at the signaling ESS because signaling costs are avoided. They suggest that begging may have initially evolved through direct sibling fighting in multiple-young broods. If fighting is condition-dependent, parents could use this information even though it was not adapted for communication, and subsequent co-evolution could then lead to the signaling ESS. Payne and Rodríguez-Gironés (1998) suggested another way that signaling might invade the non-signaling state and reach the threshold need to converge on the signaling ESS—a pre-existing receiver bias in the parent which causes them to respond to low-intensity begging behaviors.

• The Sir Philip Sidney game was used to analyze signals of need, first by Maynard Smith (1991) (discrete strategy version) and then by Johnstone and Grafen (1992) (continuous strategy version). Because this game involves a related donor and receiver of aid, it fits the parent–offspring context very well. As with the Godfray models, these models also require that signals must be costly and honest in a way that is related to true need, in order to maintain the signaling ESS. Costs could be lower if relatedness was higher. But a non-signaling ESS was again found to be a likely alternative.

• Bergstrom and Lachmann (Bergstrom and Lachmann 1997, 1998; Lachmann and Bergstrom 1998) objected to the requirement of costly signaling to achieve a signaling ESS. They proposed instead the pooling equilibria model, in which signalers over large ranges of conditions give the same class of signal (described in main text Chapter 10 section on conventional signals).

**Models combining competition and need**

**Background:**

Several models combined variation in offspring need and competitive interactions among sibs to explore the interaction of these two factors.

• Motivated by the problem of the strong non-signaling equilibrium in Godfray’s handicap signaling model, Rodríguez-Gironés (1999) expanded Godfray’s model to include competition among sibs. Three main modifications were introduced. First, unlike Godfray’s model, where total parental investment was fixed, in this model the parent can increase its provisioning rate when begging increases and vice versa. Second, offspring
competition, and not begging intensity, determines the allocation of food among the siblings. Third, the begging intensity of an offspring is not affected by the need of its sib. With these modifications, the non-signaling equilibrium disappears and the signaling equilibrium becomes stable, but signaling affects provisioning rate, not allocation.

- Johnstone (1999) expanded the Sir Philip Sidney game to include any number of competitors. Signaling could affect both the likelihood of resources being delivered and the offspring to whom they were given. Each potential recipient knows its own need but not that of its competitors, except that it is drawn from a probability distribution (there is no exchange of information among the competitors). Each recipient independently chooses a signaling level from a continuous distribution, which determines the cost it will expend. All recipients are related to the donor by the same degree. The single donor must decide whether to relinquish the resource, and if so, to which potential recipient based on their signals. If the signalers are honest, the donor should give the resource to the recipient with the most intense signal, who presumably has the greatest need. The outcome is that signaling is more likely to be profitable when $r$ is low, signaling is more profitable for very needy recipients, and the inclusion of competition decreases the overall intensity of signaling.

- Parker et al. (2002a) examined the interaction between need and competitive ability using an expanded version of the sibling competition model of Parker et al. (1989). As in the 1989 article, total parental input is fixed (parental responses don’t evolve). In addition to their inherent strength asymmetry, an additional asymmetric need or condition variable was added to the fitness equation for each sib. As in Godfray’s model, this component was included as a constant that determines the rate at which the fitness benefit curve approaches the asymptote, keeping the actual value of the asymptote equal for the sibs. Either sib could have the greater need. Costs per unit of begging are equal for the sibs, but the more competitive sib has a more effective begging display in terms of obtaining food. As in the Parker et al. (1989) article, the stronger A sib begs less but obtains more food, especially if it is the needier sib. If the weaker B sib is hungrier, it begs much more intensely and may sometimes obtain the greater share. The authors find that need and competitive ability have similar effects on begging intensity and may be difficult to distinguish in the field (Royle et al. 2002).

**Tug of war models**

Background:

Tug of war models were developed as an alternative to the transactional reproductive skew models to understand the division of reproductive benefits among cooperatively breeding individuals (Reeve and Shen 2006; Shen and Reeve 2010). In the general bordered tug of war model, two individuals compete for reproductive shares in a joint breeding effort. Their level of conflict is limited by their options for breeding outside the group. If there are good outside options, individuals will not tolerate a very high skew within the group, otherwise they will leave, so the range of conflict if the group is to remain stable is narrower than when outside options are poor. The limits of cooperation also depend on the relatedness of the two individuals. Once these “borders” for the region of stable cooperation have been established, the two individuals engage in a costly tug-of-war to compete for access to the group benefits. The two individuals are assumed to differ in dominance or competitive efficiency. The dominant can gain more benefits at the expense of the subordinate, but the costly efforts expended by both parties in this war use up a portion of the total group benefit. The ESS solution establishes the final share of reproduction for each party.

No formal tug-of-war model has been developed yet for parent–offspring conflict, but Yamamura and Higashi (1992) developed a model very much in the spirit of the tug-of-war approach. The borders of conflict are determined as before by the parental and offspring optima. This model assumes that both parent and offspring engage in costly behaviors in an attempt to achieve their optimal strategy. Any deviation by one party to move closer to their optimum results in a counter move by the other. For example, if the offspring develops a strategy to obtain more food, the parent counters by minimizing its response to the strategy. The ESS occurs where the marginal benefits of the behavioral deviations by the two parties exactly balance. The final parental investment level will lie somewhere between the two optima; it will be closer to the parental optimum if parental control is less costly, and closer to the offspring optimum if offspring can easily manipulate the parent.
Quantitative genetic models (Kölliker et al. 2005, 2010)

Context:
Genetic models evaluate the coevolutionary trajectories of parental and offspring traits and the likelihood of convergence.

Background:
When traits in one individual are influenced by traits in another individual, indirect genetic effects can play a role in their evolution. The phenotypic models discussed above do not take into account the genetic architecture of parent and offspring traits and the mutual correlations between them. For example, the fitness of offspring is affected by the combination of their own genes and the specific nesting environment generated by the parent's genes; the fitness of parents is similarly affected by the nature of their responses to the stimuli presented by the offspring traits. Certain combinations of offspring genes and parentally generated environments can result in high offspring fitness, causing particular genes expressed in parents and offspring to become genetically linked. The first attempt to apply quantitative genetic models to parent–offspring conflict found that selection on offspring traits alone can lead to linkage disequilibrium and indirect selection on maternal traits, so that the offspring trait becomes coadapted with the parental performance for that trait (Wolf and Brodie 1998). However, this model did not capture the reciprocal nature of parent–offspring interactions.

Synopsis:
- In the models by Kölliker et al. (2005, 2010), selection acts on individuals during both the offspring and the parental life stages. Solicitation behavior is expressed and subjected to selection during the offspring stage, and provisioning behavior (i.e., sensitivity to solicitation behavior) is expressed and subject to selection for those individuals that survive to breed. These traits are envisioned as evolving reaction norms.
- Selection at these two life stages is antagonistic, as offspring benefit from obtaining more resources while parents lose in terms of future fitness if they provide more resources. Lifetime fitness is modeled as survival in the offspring stage, a function of the amount of parental investment received by offspring as shown in Figure 2, and fecundity in the adult stage, a function of the lifetime number of offspring successfully raised. Offspring do not differ in competitive ability or need, there is no cost of solicitation behavior, and all offspring in a brood receive the same amount of resources.
- In the 2010 article, a third variable, baseline parental provisioning, is included as an evolving trait, along with offspring solicitation level and parental sensitivity to solicitation. A deterministic model was developed, and then stochastic simulations with mutational variation examined the changes in parental and offspring behaviors over time.

Conclusions:
- Baseline parental investment stabilizes at an intermediate level.
- Offspring solicitation and parental sensitivity become genetically correlated through co-adaptation and mutual indirect effects, dictated by the proximate mechanisms that regulate offspring demand and parental supply.
- The simulations revealed a zone of equivalent co-adaptation outcomes between solicitation level and parental sensitivity to solicitation, with these two behaviors changing rapidly and in concert over time. The dynamic character of antagonistic parent–offspring conflict may explain the diversity of provisioning strategies in different species.

Related models:
- Early genetic approaches to PO conflict employed simple two-locus models. Such models can examine
trajectories and find evolutionary endpoints, but require assumptions about genetic mechanisms that are usually not known. In the model by Stamps et al. (1978), one locus determined the offspring's level of signaling—one allele codes for a nonselfish offspring that signals for food in direct proportion to what it needs, and the other allele codes for a selfish offspring that signals for more food than it needs. The other locus determines the parent's provisioning response to the begging signal—one allele codes for a rule of feeding in direct proportion to the signal, and the other allele codes for providing less than requested. Not surprisingly, offspring are more likely to be nonselfish (honest) when the costs of signaling and selfish behaviors are high.

- In another two-locus model by Feldman and Eshel (1982), the offspring locus determines the degree of sibling competitive interaction, and the parental locus determines the degree to which the parent interferes with offspring competition. As in Stamps et al. (1978), this model leads to a range of outcomes that depend on the specific costs and benefits and net selection on the genotypes.

- Eshel and Feldman (1991) expanded on the above model with a two-locus model that examined the conditions for the spread of handicapped (honest-signaling) offspring, compared to offspring without the handicap. They allowed for linkage between the parental and offspring loci. Handicapped offspring could spread in the population if linkage was low, but not when linkage was tight. Costly signaling in this model is favored when the offspring survival function is very concave (rapid rise to the asymptote) and parents have low fertility (small brood size).

**Sibling negotiation (Johnstone and Roulin 2003)**

**Context:**

Siblings negotiate over which one should obtain the next provisioned item.

**Background:**

The models outlined above considered begging as either a signal directed at parents to inform them of the offspring's hunger level, or a form of scramble competition to gain access to the provisioning parent. Another function of begging could be to communicate with other siblings, and this interaction could even occur in the absence of the parent. For example, offspring could communicate their need to other sibs, so that less hungry sibs reduce their begging when the parent arrives with food. Or they could indicate that their need is high and that they will compete more intensely to obtain the next meal. This model thus deals exclusively with the sib–sib subgame.

**Synopsis:**

- The model assumes there are two sibs, who compete to acquire the food brought by the parent. The sibs communicate before the arrival of the parent by begging to each other, and adjust their begging and competitive behavior when the parent arrives based on the outcome of the negotiation. The model thus implies that the parent does not have complete control of food allocation.

- The offspring differ in both need and competitive ability (size). Begging is costly, but the cost of begging at a given level does not differ for the two sibs. However, the more competitive offspring can more effectively monopolize access to the parent with a given level of display than a less competitive offspring. A factor in the model specifies how easy it is to monopolize the parent, which is high in hole-nesting species where a stronger sib can push its way to the entrance and block food access by other nestmates, and low in open-nesting species where the parent can arrive from any direction.

- The hungrier sib obtains a larger marginal benefit from receiving the food than the less hungry sib. The need, or value of the food, for the two offspring varies independently according to a probability distribution.

- The model allows the level of investment in begging to the sib to evolve. Once informed of each other's needs, they then use this information to decide how vigorously to beg once the parent arrives. The analysis is a two-step process: first, to determine the level of begging in the second stage given that the sibs have provided full information about each other's needs, and then to determine the conditions under which the begging in the first
stage can honestly reflect true need.

Conclusions:

- When the food cannot be easily monopolized and offspring do not differ in competitive ability, offspring are predicted to inform the sib of their true need during the negotiation stage, and the less needy offspring is predicted to reduce its begging level during the second stage while the needier sibling continues to beg very vigorously. Half sibs are predicted to invest less in negotiation than full sibs.
- When offspring differ in competitive ability, the stronger sib is predicted to reduce its begging effort less in relation to a weaker and hungrier sib, but in the reverse situation when the stronger sib is hungrier, the weaker sib is predicted to reduce its begging effort more.
- Negotiation breaks down when it is relatively easy to monopolize the food (the stronger sib will compete for it without bothering to negotiate). Negotiation also breaks down when the food item is divisible; when it is indivisible, the siblings are more likely to negotiate and assess each other’s needs.

Parental negotiation (Johnstone and Hinde 2006)

Context:

When two parents share parental care, how should they respond to each other’s efforts?

Background:

As discussed in the main text, male and female parents are expected to disagree about their level of investment in their joint brood, as each would benefit if the other took on more of the costly effort (Trivers 1972; Maynard Smith 1977; Chase 1980; Houston and Davies 1985; Houston et al. 2005). On an evolutionary time scale, whether neither, both, or one parent should care depends on the costs and benefits of staying and leaving for the two sexes. Houston and Davies (1985) showed that biparental care is stable when a reduction in one parent’s effort selects for partial compensation (an increase) by the partner, and vice versa if one parent increases its effort. This compensatory response requires that the partners have some mechanism for communicating and coordinating their efforts. McNamara et al. (1999, 2003) suggest that conflicts of interest between two opponents should be modeled on a behavioral time scale as a series of interactions in which the parties negotiate to reach a resolution. What evolves is not a level of investment, but a stable negotiation rule, which specifies the nature of the reaction norms of each player towards the behavior of the other. Johnstone and Hinde (2006) extend this idea further in a specific model of parental coordination that also includes signals of need from the offspring. This model is therefore a male–female parent subgame with input from offspring.

Synopsis:

- Two parents provide food to their joint brood. Increasing the total provisioning by the combined parents increases total brood productivity, at the cost of future parental fitness. The benefit depends on the need of the brood, which can vary according to a probability distribution function. Parental state (condition) also varies according to independent probability distribution functions for male and female parents.
- Each parent bases its provisioning decisions on its own state (which it knows) and its estimate of brood need (which has some error). Parents may also adjust their provisioning level in response to the provisioning behavior of the partner.
- Payoff to each parent depends on the final outcome of negotiation. The analysis seeks stable pairs of linear response rules, each of which is optimal given the rule adopted by the other.

Conclusions:

- When a parent has only partial information about brood need, greater effort by the mate serves as a signal that
reduces the focal parent's error in the estimate of true brood need. This leads to a matching provisioning response by the focal parent. On the other hand, a net increase in provisioning by the mate results in a reduction in the marginal value of investment, which leads to compensatory response by the focal parent (reduced provisioning). The net outcome depends on the strength of these two opposing forces.

- When the variation in brood need is high relative to parental state, the parents are more likely to match each other’s provisioning rates, and less likely to show a compensatory response.
- Male and female parents might respond differently to each other if there is an informational asymmetry. The parent that is better informed about brood need is predicted to work harder, respond more strongly to changes in brood need, be less sensitive to the cost of provisioning, and compensate more strongly in response to changes in the partner’s provisioning effort. The poorly informed parent is predicted to match the changes in its partner’s effort.

Related models:

- McNamara et al. (2003) examined several forms of parental conflict over level of care with temporal patterns of decision-making. They find that when one parent decides about its level of care before the other and costs of care are asymmetric, the offspring may be better off with one parent than with two parents. When the level of care is reached by negotiation, there are again cases in which the offspring do better with one parent, even when costs of care are symmetric. These results differ from earlier models suggesting that two parents are always better than one (Houston and Davies 1985), but they are consistent with other models that found that offspring are likely to beg more competitively when there are two parents (Parker 1985; Mock and Parker 1997).

Literature cited


