CHAPTER 11

Synergy in social communication

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11.1 Introduction

Synergy is where a group of individuals co-ordinate to achieve a task that would not be possible were they to act alone. In social insects: the combs inside a honey bee nest (Camazine 1991), the foraging trails or labyrinth of underground tunnels of many ant species (Buhl *et al*. 2004; Franks *et al*. 1991; Theraulaz *et al*. 2003), and the thermoregulatory termite mound (Korb 2003) are made possible only by the interaction of thousands or millions of individuals. A similar observation can be made about our own human society. Without effective division of labour, specialization, and massively co-ordinated effort we would be unable to build bridges, create transport networks or organize the complex economic activity that characterizes modern society. On a smaller scale, wolves, lions and other predators hunt in groups which allows them to tackle larger prey (Packer and Ruttan 1988), while prey may be able to use their numbers to confuse predators (Treherne and Foster 1981). Although not all of these activities require communication, in many cases animals use physical, visual and chemical signals in order to co-ordinate their activities. By communicating with each other the group becomes more than the sum of its parts.

The search for food and other resources provides many examples where communicating individuals can become more than the sum of their parts. Animals often live in environments where resources are distributed in difficult to locate patches which exist only temporarily. In such an environment, a single individual has a very low rate of finding a resource patch if it searches independently. When large numbers of individuals search at the same time, however, the probability that one of them finds one of the patches is considerably larger. If these finds can be effectively communicated between individuals then the rate at which individuals find food increases. Instead of the number of individuals finding resources increasing linearly with group size, it can increase nonlinearly. The overall success of the group becomes more than the sum of each individual's success.

While it may appear that communication improves per capita success in foraging for resources, a number of challenging questions remain. As is often the case in understanding social interactions these questions are both mechanistic and functional (Krebs and Davis 1993; West *et al*. 2007). The mechanistic questions lie in studying different communication mechanisms, such as **pheromone** trails in ants and termites, dances as performed by honeybees and other **signals** and **cues**, and trying to understand how they contribute to group success. This is the question of how the effects of social communication add up. Answering this question is difficult because communication necessarily involves feedback loops, whereby information about the location of resources flows between individuals. These feedback loops can lead to complex relationships between the type of communication mechanism, the environment the animals live in and the per capita success in this environment. The first half of this chapter will review studies where these feedback loops have been identified and discuss how we have, with the help of mathematical models, come to better understand their consequences.

The functional questions are about the conditions under which communication about resources

can evolve. While the per capita success of a group might increase with the number of individuals in it, there is not always an 'incentive' on the part of an individual to communicate. If an individual does not communicate the location of a resource then it can monopolize it. Thus while there is an incentive for the average group member to have resource finds communicated, there is not necessarily an incentive for the finder to make that communication. In other words, even if per capita success would increase if all individuals engaged in social communication, this does not imply that it should evolve. There are a number of ways around this dilemma and these are discussed in the second half of this chapter. As the title of this chapter suggests, a particular emphasis is put on synergy: where non-linear increase in foraging success at the group level can lead to incentive at an individual level to cooperate and communicate about resources.

While this chapter will be divided into rather clear halves, first the mechanisms of communication and then the functional consequences, an emphasis will be put on the importance of recognizing the relationship between mechanism and function. How the effects of social communication add up has a strong role in determining why this communication evolved (Sumpter 2006). Indeed, many functional problems in understanding communication may be simply solved by a good mechanistic understanding of the role communication has on per capita foraging success (see Chapter 6 for related point regarding functional and mechanistic approaches). For example, a cornerstone of social evolution is **Hamilton's rule** which provides an inequality between relatedness and the costs and benefits of co-operation (Hamilton 1964). A common criticism, not of Hamilton's rule but of the way it might be applied in practice, is that too much emphasis is put on calculating relatedness (r) and not enough on costs (c) and benefits (b) (Korb and Heinze 2004). A mechanistic approach that recognizes that *b* and c are not constants, but instead non-linear functions of group size enables us to come to a better understanding of why different forms of social communication evolve in different types of groups. It allows us to bypass much of the abstract, difficult and often unproductive discussion about which level of selection operates and instead concentrate on making empirically testable predictions.

11.2 Mechanisms

Social communication about resources usually occurs between animals which live in a communal nest or den. Communal living provides a good opportunity for transfer of information about the location and quality of resources. Individuals that have found food possess information about where it is located. If successfully communicated, this information can be used by nestmates who can then locate the same food source. This communication can be either through cues, which are "a feature of the world that can be used by the receiver as a guide to future action" (Maynard Smith and Harper 2005) or signals which are "an act or structure that alters the behaviour of another organism, which evolved because of that effect, and which is effective because the receiver's response has also evolved" (ibid) (See also Chapter 1). In this chapter we consider mainly evolved signals. In **eusocial** insects, sophisticated signals have evolved to actively communicate food discoveries, but signals are also found in, for example, cliff swallows as well as other species of birds and mammals.

11.2.1 Ant pheromone trails

Many species of ants deposit pheromone signals marking the route from food to nest (Hölldobler and Wilson 1990; Wilson 1971) (see Chapter 5 and 7 for related discussion on pheromones). These trails allow other ants within the nest and those already exploring to find the food source. As more ants find the pheromone trail and, as a consequence, the food source, a positive feedback loop is started. The pheromone trail is strengthened and after a short time a steady trail of ants is established between food and nest. Pheromone trails are formed purely on the basis of local information. They are started by a single individual or a small group of ants responding to the presence of food and they are reinforced by ants that encounter and successfully follow the trail.

A striking aspect of pheromone trail recruitment is that it needs a minimum number of participants

in order to function. A study of the foraging efficiency of different sized Pharaoh's ant colonies revealed that the number of ants arriving at a feeder placed a short distance from the nest increased as a non-linear function of colony size (Beekman *et al*. 2001). Figure 11.1a shows how foraging success changes with colony size for these ants. Below a critical colony size the foragers functioned independently of one another. When the feeder was presented to small colonies there was no increase in the number of ants visiting the feeder. Above the critical size however there was a sudden switch to effective foraging by the ants, and the number of ants visiting the feeder increased with colony size. Similar results, although with a smaller number of colony sizes have also been observed in Argentine ants (Halley and Burd 2004).

Why does foraging success increase non-linearly with colony size? We can answer this question by thinking about what happens when an ant in a colony of a particular size finds food. If an ant in a small colony finds a food source a long way from the nest, then by the time another ant passes over the place she left pheromone trail, the pheromone will probably have evaporated. In this case, the trail doesn't help other ants find the food. For large colonies of ants, however, it is more likely that an ant will find the pheromone trail before it evaporates, follow it and thus reinforce it. Beekman *et al*. (2001) formalised this argument in a differential equation model of the mechanisms underlying pheromone trail laying. Their model is given in Box 11.1. The key assumptions of the model are that the rate of individual ants joining a trail is an increasing function of the number of ants on the trail, while the rate of individuals losing the trail is a decreasing function of group size. In this model a *bifurcation* occurs whereby at a critical colony size foraging trails become effective (Figure 11.2).

While the effect of colony size on foraging success has been investigated in these short time scale experiments, less is known about the long term fitness consequences of using pheromone trails. In general, the study of per capita 'lifetime' productivity of ant societies has been focused on the early stages of colony foundation, where increases in productivity are usually attributed to co-operative building and defense than to foraging success. One of these studies that could relate to information transfer looked at brood raids by fire ants on other nearby ant colonies. Adams and Tschinkel (1995) found that nests consisting of multiple queens produced more workers and then had an increased success during raids on other colonies. Further work is required in this area, especially to link foraging efficiency to colony growth and fitness measures.

Pheromone trails act not only to inform nestmates where food is located, but can also be used to find the shortest path to it. For example, Beckers *et al*. (1992) presented starved colonies of the ant *Lasius niger* with two alternative bridges of different lengths between food and nest. In these experiments, individual ants made little or no comparison of the two bridges, instead the slightly longer trip time means that pheromone builds up slower on the longer bridge. Thus when trail following ants make the choice between two bridges they detect a higher concentration of pheromone on one of the bridges, i.e. the shorter one (Beckers *et al*. 1993). The shorter bridge is chosen with a higher probability by the follower ants and when these ants return home they further reinforce the shortest path.

Theoretical studies have shown that effective group-level decisions about which of several paths to food is shortest also require a minimum number of ants (Nicolis and Deneubourg 1999; Nicolis *et al*. 2003). Once an equilibrium flow of ants has been reached on the bridge, ants in small colonies will choose bridges in proportion to the respective lengths of the bridges, while ants in large colonies will be strongly biased towards the shortest bridge. Thus although in both cases the ants are capable of choosing the shortest path, ants in large colonies focus their workforce more strongly on the shorter bridge. Similar results apply when ants are choosing between two food sources of different quality, ants are more likely to lay a pheromone trail to a better quality food source (Sumpter and Beekman 2003). These studies suggest that larger colonies are likely to be able to build more efficient pheromone trail networks, leading to better quality food sources. Per capita foraging success will thus increase with group size.

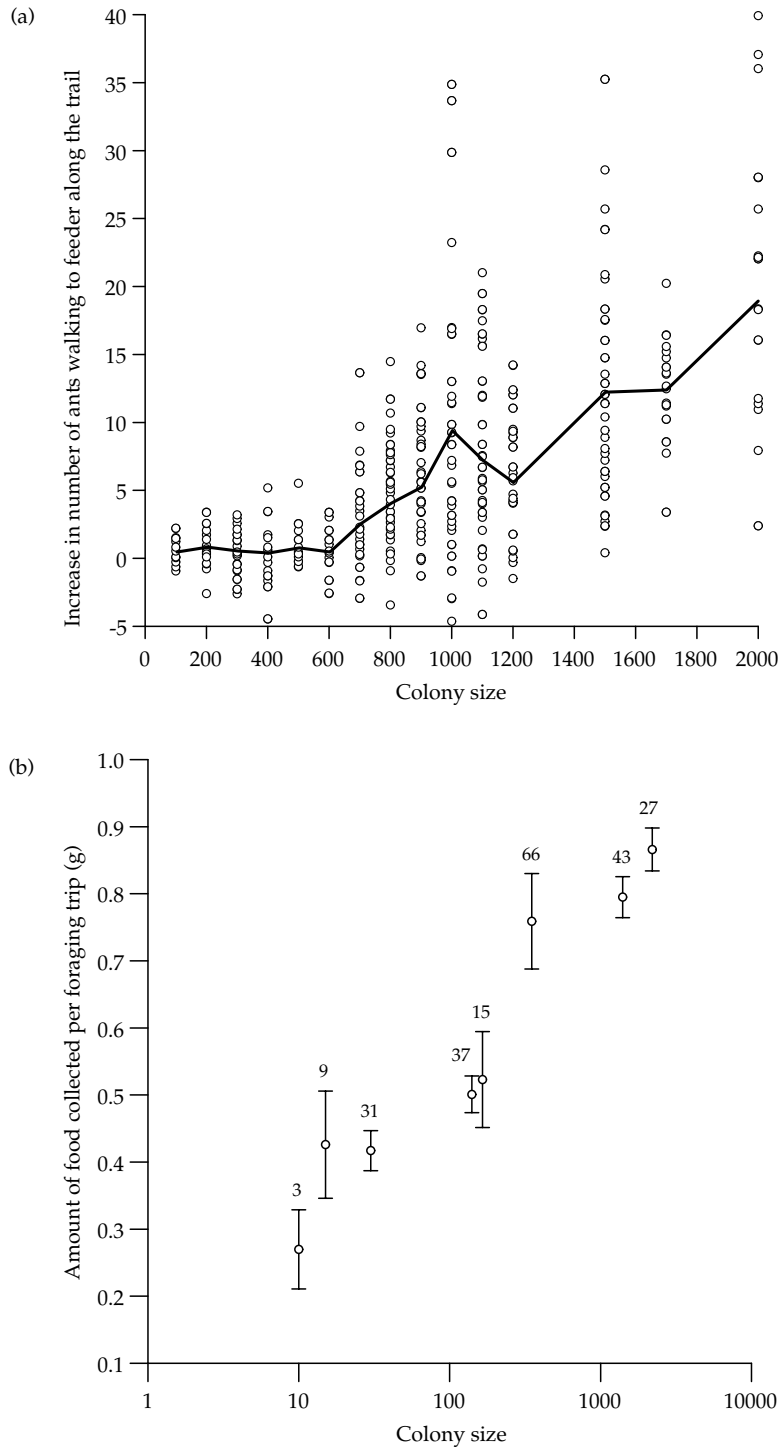


Figure 11.1 How foraging success increases with group size for ants and sparrows. (a) colony size vs the maximum increase in the number of ants walking to a feeder within 40 minutes of its introduction to an arena containing a starved ant colony (see Beekman *et al.*, 2001 for details). The solid line connects the means of all trials at a given colony size, while crosses represent single trials. Reproduced from Beekman *et al.*, 2001. (b) group size vs per capita foraging success. The figure shows how the amount of food collected per parent cliff swallow increases with the size of colony the swallow lives in. Reproduced from Brown and Brown 1996.

Box 11.1 Mechanistic models of foraging

General framework

Here we give a simple mechanistic model, based on a framework provided by Sumpter and Pratt (2003), of how a group of communicating foragers find a food source. We assume a group of n individuals and let x be the number of these individuals that are informed about where the food source is. Thus x is a measure of group productivity, since it is the number of individuals successfully foraging at any point, and x/n is the per capita success since it is the proportion of informed individuals in the group.

We assume that social communication increases the rate at which individuals find a food source. We denote the rate per individual of finding the feeder with $f(x)$ which is an increasing function of x. This function f differs depending on the recruitment mechanism used by the modeled species. We denote the rate per individual of losing the food source as $g(x)$ which again differs dependent on the mechanism by which individuals lose the feeder. We thus denote the rate of change of the number individuals going to the feeder as

$$\frac{dx}{dt} = f(x)(n-x) - g(x)x$$

where t denotes time. Solving

$$f(x_*)(n-x_*) = g(x_*)x_*$$

for x_* gives the equilibrium, or long term, number of individuals going to the feeder. It is by finding how this equilibrium changes with n that we determine how foraging efficiency changes with group size.

Pheromone trail communication

Beekman *et al.* (2001) use a version of this model to look at pheromone foraging ants. In this case, x denotes the number of ants on a pheromone trail to a feeder. They set

$$f(x) = \alpha + \beta x$$

where α is the rate at which individuals find the food source in the absence of a trail and βx models the fact that the number of ants finding the food source increases with the number leaving a trail to it. They further set

$$g(x) = \frac{s}{K+x}$$

which is a decreasing function of ants on the trail.

The equilibrium number of individuals on the trail to the food source is given by

$$\alpha(n-x_*) + \beta x(n-x_*) = \frac{sx_*}{K+x_*} \qquad \text{(A.1)}$$

Figures 11.2a and 11.2b shows how x_* changes with n for two different values of α. When random finds of the feeder are frequent (Figure 11.2a) then there is a unique stable equilibrium. When random finds of the feeder are infrequent (Figure 11.2b) there is an intermediate range of values of n at which there are two stable equilibrium. In both cases the number of individuals visiting the feeder, i.e. foraging success, is a non-linear increasing function of the number of foragers. Figures 11.2c and 11.2d shows that in both cases there is a range of group sizes at which per capita foraging success also increases with group size.

Dance communication

Beekman *et al.* (2007) propose that with dance communication the rate at which bees find a feeder can be written as

$$f(x) = \alpha(1-a/A)^{px} + \beta\left(1-(1-a/A)\right)^{px}$$

where A is the total area of the honey bee colonies dance floor, a is the area covered by a single dancing bee and p is the proportion of time that a foraging bee spends dancing during a round trip to the feeder. The expression $1-(1-a/A)^{px}$ is the probability that an uninformed bee can find a dancing bee to follow (Beekman *et al.* 2007). α and, respectively, β are the rate

continues

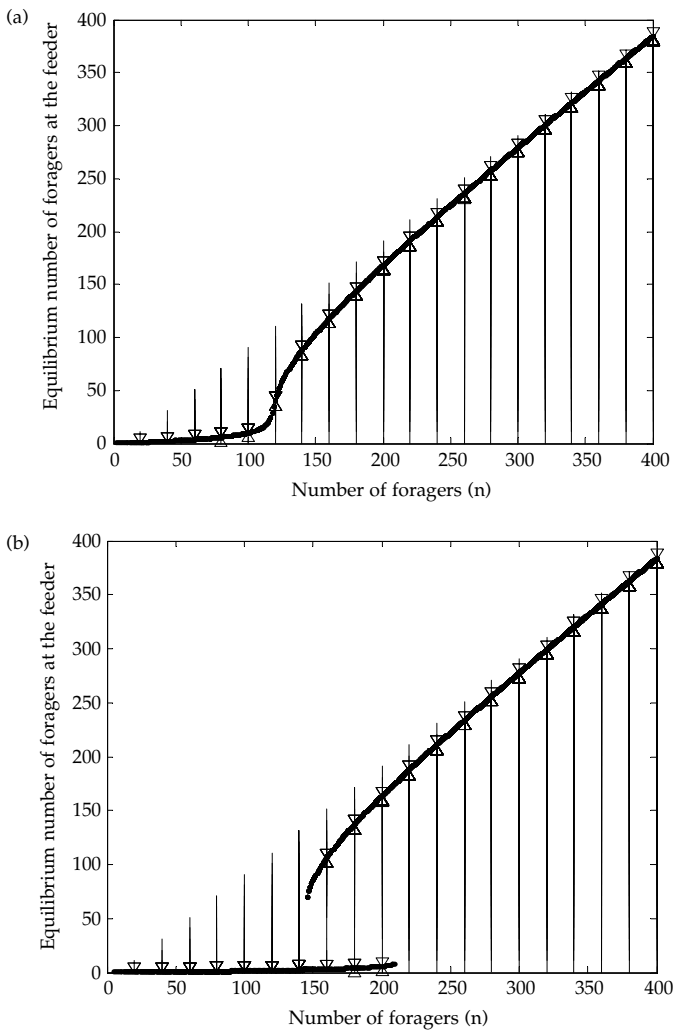
Box 11.1 ***continued***

at which bees which could and, respectively, could not find a dance to follow find the food source. The rate at which honey bees retire from following is independent of the behaviour of other foragers, so that $g(x)=\lambda$.

The equilibrium number of bees going to the food source is thus given by

$$\left(\alpha(1-a/A)^{px}+\beta\left(1-(1-a/A)\right)^{px}\right)(n-x)=\lambda x \qquad \text{(A.2)}$$

Figure 11.3a shows how x_* changes with n for some typical parameter values. In this case there is only one stable equilibrium for the number of foragers going to the food source. The foraging success is a non-linear increasing function of the number of foragers, although not as dramatic as that for the ants. Figure 11.3b shows that there is a range of group sizes at which per capita foraging success also increases with group size.



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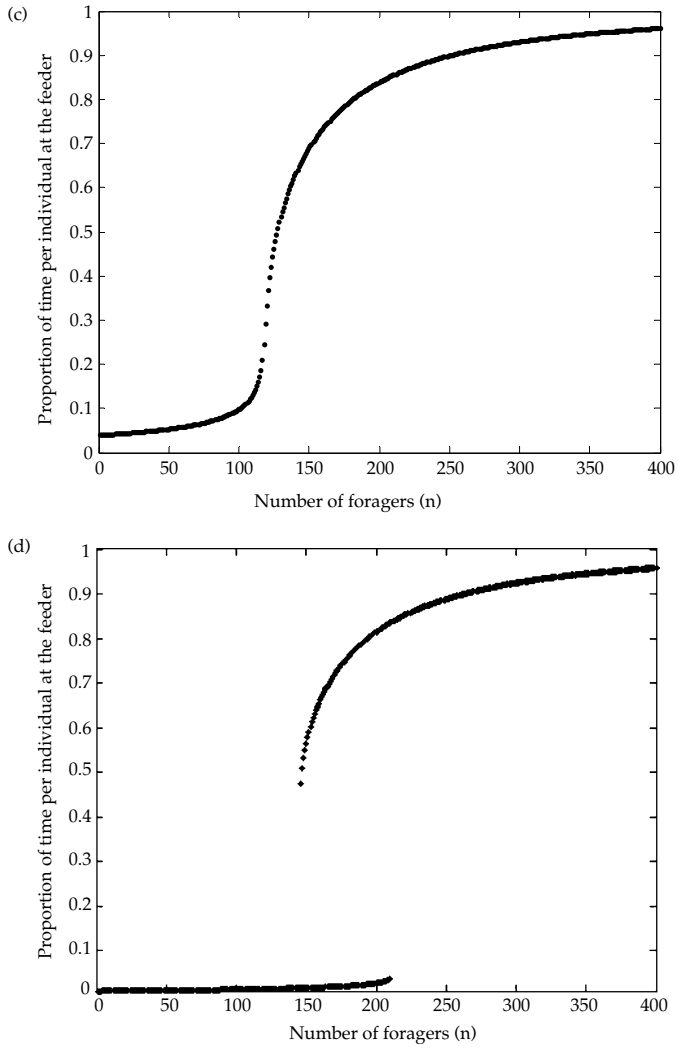

Figure 11.2 Prediction of model given by equation A.1 (see Box 11.1 for details) of how the number of foragers using a trail to food changes with number of foraging ants in the colony in two different cases (a) when random finds of the food source are common ($\alpha = 0.004$) and (b) when random finds are rare ($\alpha = 0.001$). The black lines give the predicted stable equilibrium for number of foragers visiting the feeder. The arrows indicate which equilibrium occurs given different initial number of ants at the feeder. The per individual proportion of time on the trail is shown for (c) frequent and (d) infrequent finds. Note that the dark lines in (c) and (d) are simply the lines on (a) and (b) divided by the number of foragers. Other parameter values are $\beta = 0.00015$, s = 1 and $K = 10$. See Sumpter and Pratt (2003) for details of the analysis of this model.

11.2.2 Honey bee dances

One of the most comprehensively studied forms of social communication about resources is the waggle dance of the honey bee (Seeley 1995; von Frisch 1967). Waggle dances are performed by honey bee foragers that have found highly rewarding nectar or pollen sources, and inform nestmates about the location of these resources. Uninformed bees in the hive follow a dance and then fly in the direction of and for the distance encoded by the dance, after which they search locally using odour and visual cues (Riley *et al*. 2005). Usually a recruited bee will fail to find the advertised food site, but by repeatedly returning to the dance floor and following further dances she will eventually find and return with food (Seeley and Towne 1992). Since recruited bees may later perform dances themselves, the waggle dance, like pheromone trails, acts as a positive feedback mechanism through which information about food is transferred.

Theoretical predictions about how foraging success changes with colony size are different for dance communication than for pheromone recruitment.

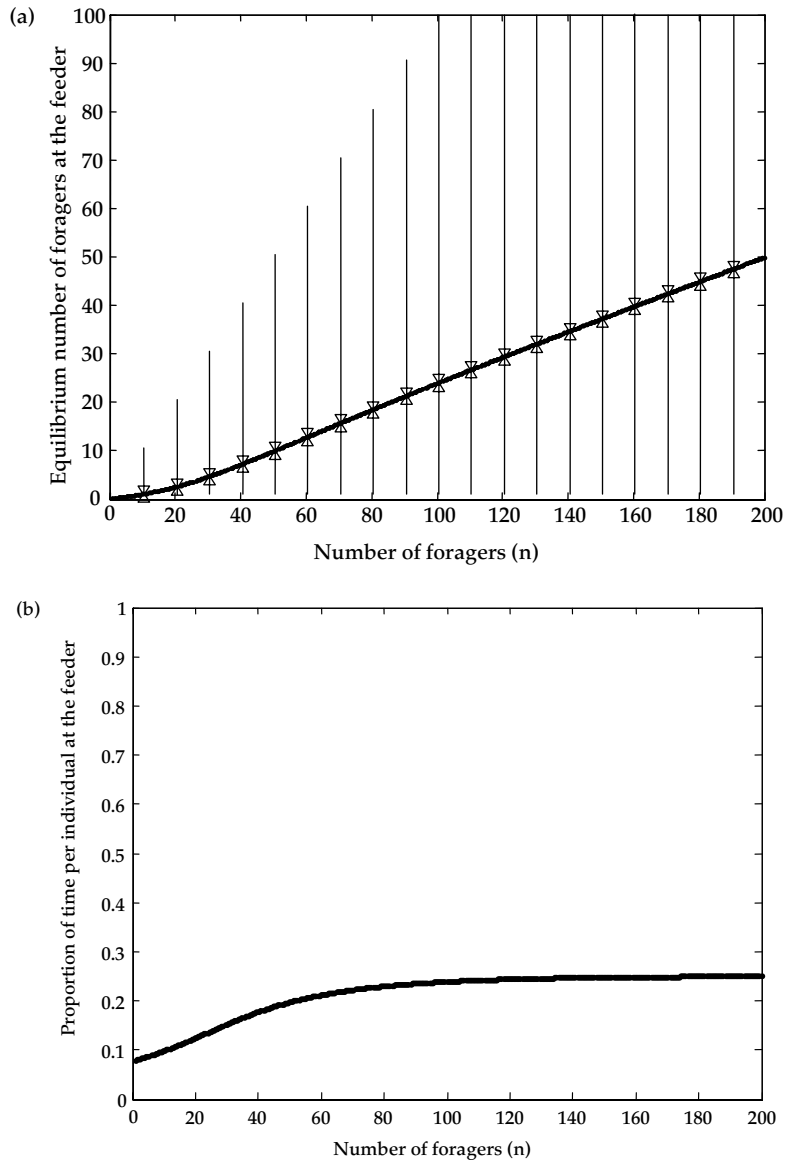

Figure 11.3 (a) Prediction of model given by equation A.2 (see Box 11.1 for details) of how the number of foragers visiting a feeder changes with number of foraging bees in the colony in two different cases. The black lines give the predicted stable equilibrium for number of foragers visiting the feeder. The arrows indicate which equilibrium occurs given different initial number of ants at the feeder. (b) The per individual proportion of time spent at the feeder.

The difference between the two forms of recruitment arises from the functions with govern rates of recruitment and retirement from a food source. The rate at which bees are recruited to food is, like the pheromone recruiting ants, an increasing function of the number dancing for the food. However, unlike the ants, the decision by a bee to retire from a food source is made independently of the number of other bees foraging and purely based on the quality of the source (Seeley 1995). Thus rather than

retirement rate per individual decreasing with the number of individuals at the food source it is a constant, independent of the number of other foragers. Box 11.1 investigates how independent retirement affects foraging success. As with the ants, foraging success is a non-linear function of colony size although it is less dramatically so than it is with the ants (Figure 11.3). Very small colonies lose out because potential foragers have difficulty locating dances to follow. This result is also obtained in more detailed individual based models of honey bee foraging (Dornhaus *et al*. 2006).

Rather than concentrating on the role of colony size, experimental work on the efficiency of the honey bee dance has looked at the environmental conditions under which dance communication provides a fitness advantage (see Chapter 10 for discussion of another environmental factor, parasites, and their role in collective behaviour). Perhaps surprisingly, given the interest in the evolution of this communication mechanism, the waggle dance does not always result in more efficient foraging by the bees. Sherman and Visscher (2002) found that the dance only provided an advantage, in terms of colony weight gain, during winter months when food was scarce. For the majority of the year, honey bees in hives within which all dance information was disorientated gained weight at a rate not significantly different than control colonies in which dances could be followed as usual. Dornhaus and Chittka (2004) found that in temperate habitats, similar to those in Sherman and Visschers' experiment and in which food is relatively abundant, dance communication again offered no improvement in foraging efficiency. In tropical habitats, however, where food is more tightly clustered, they found that dance disorientated colonies performed worse than control colonies. The dance appears to play an important role in colony survival in circumstances where food is difficult to find and/or highly clustered. Beekman and Lew (2008) used a model to show that if a dancing and no-dancing colonies of bees compete locally for resources, the dancing bees can rapidly monopolise high quality food sources.

One study that did look at the role of colony size in honey bee foraging was conducted by Beekman *et al*. (2004). They looked at how the number of patches visited by bees differed between large and small colonies. Although the number of foragers in these colonies was proportional to colony size, there was little difference in the number of distinct foraging sites danced for by small and large colonies. In other words, foraging was less focused on particular sites in small colonies. One interpretation of these results is that small colonies are unable to focus their foraging on particular sites because there are insufficient dances to efficiently communicate food finds. As a result, the bees in small colonies forage independently of one another and do not benefit from communication about profitable food sources. This hypothesis is supported by experiments in which the number of dances performed within the hive was manipulated (Beekman *et al*. 2007). When there were fewer dances to follow bees scouted independently of each other.

11.2.3 Birds and rodents

Recruitment signals are not limited to social insects. For example, Norway rats deposit odour trails from where they find food back to the nest (Galef and Buckley 1996) (see also Chapter 6). By attracting nestmates, these trails spread information about widely scattered, ephemeral food sources. Naked mole rats also leave odour trails on finding food, make chirping noises during their return trip and display the collected food for nestmates (Judd and Sherman 1996). There is evidence for a weak form of positive feedback with follower naked mole rats vocalising when they find food, but with a lower probability than the initial discoverer. Recruited mole rats appear to look for the trail left by a specific individual, suggesting that recruitment to a particular food source is proportional to the number of recruiting individuals. This would suggest that the improvement in foraging efficiency with group size is more likely to be similar to that predicted for the honey bees (Figure 11.3) than the ants (Figure 11.2).

Cliff swallows nest in colonies at which there is communication about the location of food (Brown and Brown 1996). At the nest this communication is primarily cue-based, with birds that successfully return with food being followed by their

nestmates. There is no evidence that successful birds actively advertise food finds at this stage, i.e. communication is cue-based, but there is also no evidence that they disguise these finds. Clear evidence of signalling between birds is however seen in the form of food calling at mobile insect swarms. The signalling birds can track the swarm while being able to make return journeys between the colony and the insects. Brown *et al*. (1991) suggest that cliff swallow signals about food location occur only when the insects upon which they feed are spatially clustered. Indeed, in other contexts sparrows only signal the location of food when it is sufficiently large that it can be shared with other birds (Krebs and Davis, 1993).

When naïve North American ravens were added to communal roosts they followed their informed roost-mates to new feeding sites (Marzluff *et al*. 1996). At the beginning of these flights some birds produce noisy 'kaws' and 'honks', although it is not known whether these are more often produced by informed birds. There is however evidence based on a small number of observations of European ravens that the first birds to be seen at a bait carcass were also those that performed flight displays and vocalisations the evening before and appeared to initiate morning departures from the roost (Wright *et al*. 2003). These observations would suggest that informed ravens actively signal the location of food.

While these examples provide evidence that signaling and social communication exist in a wide range of species, less is known about how the effects of these forms of communication add up. There are however some noteworthy exceptions. For example, it is known that signalling by Norway rats reduces the time it takes individuals to find food (Galef and White 1997), although it is not clear how foraging success changes with group size or the number of trail layers. Foraging success and group size has been studied in cliff swallows. Brown and Brown (1996) found that both the amount of food collected by parent cliff swallow per foraging trip and the frequency of these trips increased with group size. Although each of these factors appeared to increase log linearly with group size (Figure 11.1b), when combined using least squares regression they appeared to add up to a linear increase in per capita success with group size (Brown and Brown 1996).

11.3 Function

Why have animals evolved to communicate with each other about food finds? All of the examples above involve an apparently costly signal between the individual which has found food and those which have not. The cost can be either a direct result of the time or energy expended in making the signal, e.g. in performing a dance or producing pheromone chemicals, or a result of increased competition for the resource signalled for. In order for a costly signal to have evolved there must also be an associated benefit (Maynard Smith and Harper 2005). This benefit must on average be greater than the cost. The key evolutionary question about all systems where we see costly signalling is: what are the benefits of communication?

Such questions do not usually have one simple answer but depend on a whole range of factors. Here, we discuss three types explanations: **inclusive fitness**, synergy and reciprocation. A particular emphasis will be put on synergy, because it arises in situations where foraging success increases as a non-linear function of the number of individuals involved. Indeed, synergistic co-operation requires a good understanding of the mechanisms underlying co-operation.

11.3.1 Co-operation between relatives

The basic idea of inclusive fitness theory as an explanation for the evolution of helping is that genes which promote costly helping towards relatives are likely to be selected for because these relatives have a higher probability than a randomly selected member of the population of carrying the same gene by decent as the helping individual (Hamilton 1964). The gene is passed through the generations not directly but indirectly through these relatives, who because they were helped have a greater reproductive success than individuals without relatives to help them. Thus, in assessing the fitness of a gene we must account for its inclusive fitness, the direct benefit (which may be a negative, i.e. a cost) it gives the individual plus the indirect benefit it gives to

relatives (West *et al*. 2006). Social communication about the location of food to relatives can confer indirect fitness benefits to other individuals in the foraging group or to a small group of reproductive individuals. Many social insect species have a high degree of within group relatedness and inclusive fitness is thought to contribute to the evolution of social communication of these species (Bourke and Franks 1995; Foster *et al*. 2006). Indeed, the importance of inclusive fitness is firmly established in evolutionary biology and is the focus of several chapters in this book.

When individuals gain inclusive fitness by co-operating then it is useful to consider what types of communication are best for the group as a whole, rather than for which are best for each individual. The observation that small colonies of ants cannot effectively forage using pheromone trails has interesting consequences for the evolution of communication mechanisms within these colonies. Pheromone trail laying has evolved primarily in ant species which contain large numbers of workers (Beckers *et al*. 1989), with ants that typically live in smaller colonies using tandem running or group recruitment where either another individual or a small group of individuals is directly guided towards the food source found (Hölldobler and Wilson 1990). Furthermore, *Lasius niger* ants change their trail laying behaviour dependent on their colony size (Devigne and Detrain 2002). Ants in small colonies do not leave trails, while those in large colonies do.

11.3.2 Synergy

Consider an animal foraging for food which is located in a difficult to find clump, but with large capacity once it is found. We assume that if a focal individual finds food and communicates its location to its partner then the partner can find the food. Meanwhile the focal individual, which has a limited capacity for how much food it can carry, returns to its nest to feed its offspring. In order for the focal individual to locate the food source again however the partner must also communicate its location. For example, we can imagine a situation where it is difficult to reliably navigate to the food source or that it changes position through time. If the link of communication is broken the food becomes difficult to find again.

To illustrate this idea, we can describe this situation as a two player game where individuals have one of two phenotypes: 'Communicate' or 'Do nothing'. The payoff table for this game is given in Table 11.1. If the focal animal communicates the presence of food it pays a signaling cost C but gets a direct benefit, from for example predator dilution, D. The partner gets benefit B irrespective of whether it signals itself or not, but if it signals it pays cost C. If both signal then both individuals get an extra benefit, E. This extra benefit is acquired because both individuals signal food location and thus are always able to find the food source again after they return to the nest. The term E makes the animals interactions more than the sum of its parts. It arises only when they both communicate.

Assuming that the direct benefit, D, is less than the cost, C, but the extra benefit E is greater than the cost, i.e. $E>C>D$, then there are two evolutionarily stable states for this game. If a focal individual lives in a population where everyone cooperates then it is always better to cooperate, since $B+E-C>B$. However, if the focal individual lives in a population where everyone defects then, because $C>D$, it is better to also defect and avoid a negative payoff. Thus, the two possible evolutionarily stable states are one corresponding to everyone co-operating and another corresponding to

Table 11.1 Payoff table for two player social communication game. The values in the table determine the fitness gained by the focal individual as a function of its own strategy and that of its partner. For a model of synergy we assume that $E>C>D$.

Focal/Partner	'Communicate' (Cooperate)	'Do nothing' (Defect)
'Communicate' (Cooperate)	$B-C+E$	$D-C$
'Do nothing' (Defect)	B	0

everyone defecting. Which evolutionarily stable state the population evolves to depends on the initial conditions. If the population initially contains more than C/E co-operators then evolution will lead to full co-operation, otherwise evolution will lead to full defection.

A counter-intuitive prediction of this model is that costly behaviour can evolve even when the focal individual gets no benefit from co-operating when interacting with other individuals that defect. This point is not always given full consideration when discussing the evolution of costly signals. For example, cliff swallows call to signal the location of insect swarms thus paying a, probably small, cost but provide nearby foraging partners a positive benefit in finding food. Brown *et al*. (1991) suggest, quite correctly, that swallows may have evolved call signalling because "even if other birds do not also call, the caller could benefit through local enhancement simply by watching the nearby group members as some of them track the subsequent movement of the prey". If this is the case, then there may be no cost to interacting with a defector, i.e. $D > C$, and full co-operation always evolves even in a population of defectors. However, our model suggests that a direct benefit of signalling is not a requirement for the evolution of food calling. Rather, the model predicts that provided there is an extra benefit when both birds call that is greater than the cost of calling, then co-operation can evolve independent of any direct benefits in the absence of calling, i.e. $B < C$. It is plausible that such extra benefits exist for cliff swallows. Groups that contain individuals that always signal can continuously track the movement of insect swarms. When interacting with a co-operator the focal individual gets the additional benefit, $E > C$, of being able to refind its own discovery. Defection would reduce both the focal and the partner birds' ability to find food.

The last paragraph takes a two player game and suggests it may apply to multi-player interactions. Swallows don't forage in pairs but rather in large groups. Under what circumstances can synergistic co-operation persist in larger groups? Box 11.2 describes a continuous strategy game with group size N in which each individual can make an investment p_i in communicating. This investment incurs a cost, but group productivity increases as a function of the total communication by the group. This productivity is shared equally between individuals, so benefit to an individual increases as productivity divided by number of group members. Co-operative communication is evolutionarily stable for large groups in this model provided that group productivity increases as at least the square of the group size, or equivalently provided that the benefit per individual increases at least linearly with group size.

Clearly group productivity cannot increase indefinitely with group size. Once the group is so large that any exploitable food sources are quickly exhausted, then it is no longer beneficial to signal about its location. By the time signalling individuals return to the food source it will have been consumed by all the other group members. Figure 11.5 shows how the evolutionarily stable states change with group size with a productivity function which first increases non-linearly then only linearly with group size. For small groups there is an evolutionarily stable state where all individuals cooperate, but as the group becomes too large this becomes unstable and all defect is the only evolutionarily stable state. The important message here is that when resources are sufficiently large but difficult to find then co-operation can evolve.

Cliff swallows nest in colonies of genetically unrelated individuals and inclusive fitness plays little or no role in the evolution of their foraging behaviour. In Figure 11.1b we saw how per capita delivery of food to the nest changes as a function of group size for cliff swallows. Although it is not entirely clear whether this increase is equal or greater to linear, as would be required under the model in Box 11.2, the fact that an increase is seen suggests that the swallows interactions could be synergistic. The evolution of these signals, and others seen in rats and other birds, is intimately linked with positive feedback. Signalling by a focal individual improves other group members' chances of discovering food and since these group members are also signallers then this then improves the chance of rediscovering the same food or finding other nearby sources. The positive feedback continues and group productivity increases as more than the sum of the group's parts.

Box 11.2 Synergy in groups of size N

Consider a population that on each generation randomly aggregates in isolated groups of size N. Each individual can choose to invest an amount $p_i \in [0, 1]$ in a co-operative behaviour. The benefit to each individual, $g(\sum_{j=1}^{N} p_j)/N$, is assumed to be a function of the overall productivity of the group members, g, divided by the total number of group members. We assume that this function is the same for all group members. Thus the payoff for an individual i is

$$\frac{g\left(N, \sum_{j=1}^{N} p_j\right)}{N} - p_i c$$

where c is the cost of the co-operative behaviour. This model is an example of a structured-deme model (Nunney 1985; Wilson 1983). Here, we further assume that productivity increases as some power α of the level of co-operation of, i.e. $g(P) = bP^{\alpha}$.

We now follow the method outlined by Doebeli *et al.* (2004). Assume that all individuals have the same strategy q apart from a mutant with strategy p. The selection gradient is then

$$D(q) = \frac{\partial}{\partial p}\left(\frac{b}{N}(p + (N-1)q)^{\alpha} - cp\right)\Bigg|_{p=q} = \frac{b\alpha}{N}(Nq)^{\alpha-1} - c$$

Since we insist that investment is between 0 (defection) and 1 (co-operation), we can evaluate the selection gradient at these two extremes in order to see whether they are stable strategies. Evaluating $D(0) = -c$ tells us that the all defect is an evolutionarily stable state. Similarly, $D(1) = b\alpha N^{\alpha-2} - c$ tells us that the all cooperate is also evolutionarily stable, provided $b\alpha N^{\alpha-2} > c$. When all cooperate is stable there exists, although we don't determine it explicitly here, a single steady state q_* between these two extremes which is not convergent stable. This steady state acts as a repellor: when initially $q > q_*$ then $q \to 1$ and when initially $q < q_*$ then $q \to 0$. Qualitatively, the situation is the same as in the two player discrete game discussed in the text: both all cooperate and all defect are evolutionarily stable.

The condition for synergistic co-operation in this model is $b\alpha N^{\alpha-2} > c$. If $\alpha < 2$ then as group size increases the cost an individual is willing to pay in co-operating decreases. For example, when $\alpha = 1$ we recover $b/N > c$. If $\alpha \geq 2$, however, then as group size increases the cost an individual is willing to pay tends toward a positive but finite limit. In particular, when $\alpha = 2$, co-operation is stable if $2b > c$ independent of N. Figure 11.4 shows how the steady states change with group size for $\alpha = 3$.

Figure 11.5 shows similar analysis for $g(P) = T^2 \frac{P^3}{T^2 + P^2}$. This productivity function initially grows cubically, but when group size exceeds T the growth becomes more linear. For large P growth is purely linear. Here there are three different parameter regimes. For very small group sizes all individuals evolve to invest nothing ($p = 0$) in co-operation, but as group size increases the strategy of full investment ($p = 1$) becomes stable. At intermediate group sizes the full investment becomes unstable and a compromise of partial investment becomes stable. As group size increases still further all communication becomes evolutionarily unstable and $p = 0$ is the only evolutionarily stable state.

Synergism is likely to combine with inclusive fitness in promoting co-operation. Several authors have argued that because relatedness within social insect colonies is lower than first predicted, inclusive fitness may have a less important role in co-operation than once supposed (Korb and Heinze 2004; Wilson and Holldobler 2005). It is here that the observation that signalling in foraging increases per capita foraging success with group size plays an important role. In terms of Hamilton's rule, synergism leads to an increase in benefits and thus a lower requirement for within colony relatedness for the evolution of co-operation. For naked mole rats, the relevance of high within

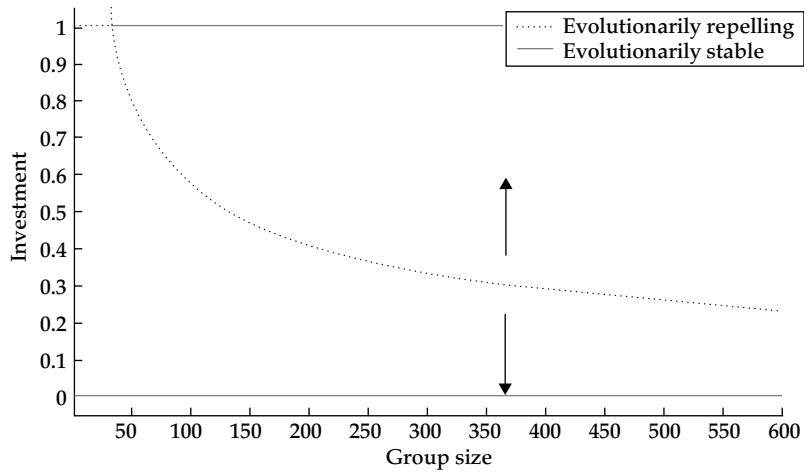

Figure 11.4 Model of synergy described in Box 11.2 with productivity that increases with the cube of group size, i.e. $g(P) = bP^3$. Bifurcation plots showing the location and stability of interior singular strategies and boundary points as a function of group size *N*. We choose $c/b = 100$ so that for very small groups there is no benefit to co-operation, i.e. $p = 0$ is the only stable strategy. With increasing group size a repelling interior singular strategy emerges and both no investment ($p = 0$) and maximal investment ($p = 1$) are locally stable strategies. Arrows indicate for which initial investment in co-operation these strategies will evolve.

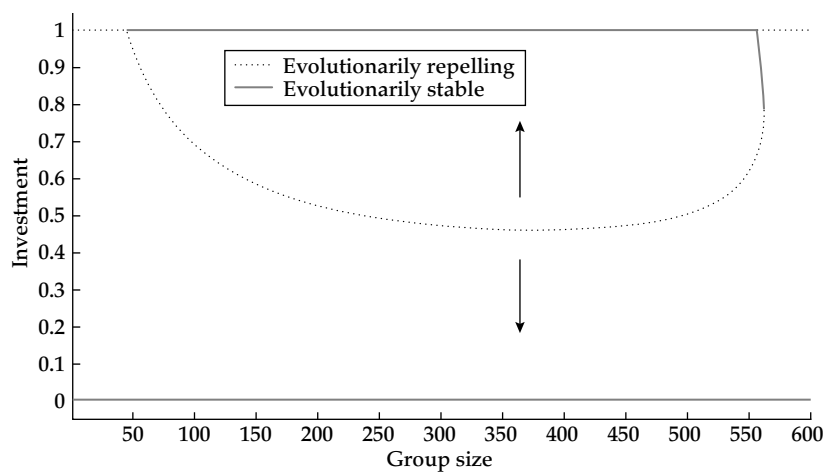

Figure 11.5 Model of synergy described in Box 11.2 with group productivity that first increases with the cube of group size but later saturates to linear increase, i.e. $g(P) = bT^2 \frac{P^3}{T^2 + P^2}$. Parameters are $c/b = 5$ and $T = 40$. Bifurcation plot showing the location and stability of interior singular strategies and boundary points as a function of group size *N*. As in Figure 11.5 with increasing group size a repelling interior singular strategy emerges and both no investment ($p = 0$) and maximal investment ($p = 1$) are locally stable strategies. In this case however as group sizes increases further $p = 1$ becomes unstable and a strategy corresponding to an intermediate investment in communication becomes stable. As group size increases still further the intermediate investment strategy disappears and $p = 0$ is the only stable state. The arrows from points indicate for which initial investment in co-operation the various stable strategies will evolve.

group relatedness (Reeve *et al*. 1990) has been questioned because the degree of competition between relatives has not been measured (Griffin and West 2002). With or without competition for resources, synergism whereby co-operation increases the amount of available resources could lead to the evolution of signalling during foraging. Further empirical tests of the foraging performance of

different sized colonies are needed to clarify the relationship between synergism and relatedness for these species.

Synergy plays a role at all levels of biology. While we have used animal groups to illustrate these ideas, it is perhaps at the level of microbiology that synergy plays its most important role (Maynard Smith and Szathmáry 1995). In Chapter 2, Diggle *et al*. give an overview of quorum signaling and sensing performed by bacteria. Here we see a wealth of examples where group productivity is a non-linear function of the local density of co-operators. For example, the pathogenic bacterium *Pseudomonas aeruginosa* produces costly siderphores which act to release iron from the host organism (Harrison and Buckling 2005). The production of siderphores is only effective when they are produced in sufficient quantities: siderphore production below a threshold level will have little effect in releasing iron but above this threshold iron will be effectively released promoting growth of the bacteria (A. Buckling, personal communication). As in ant foraging, a minimum threshold of signalers is required for the co-ordinated action to succeed. We would predict that if typical group sizes were close to that of the minimum threshold of signalers then full co-operation can evolve without invoking inclusive fitness arguments. As with social insects, there may be a degree of between individual relatedness within hosts that further promotes co-operation. Synergy and inclusive fitness effects can interact to promote co-operation.

11.3.3 Reciprocal interactions

Of the examples of social communication in foraging given in the previous section, the one for which it is hardest to provide a functional explanation based on either synergy or inclusive fitness is the flight displays by ravens (Wright *et al*. 2003). These displays lead non-relatives directly to food items that have only a limited capacity and do not suffer from a large predation risk. For these birds, groups may be sufficiently small that repeated interactions, either in terms of direct reciprocation or indirect reputation building, could play a role in their evolution. In general, reciprocal interactions can occur when groups are small and repeated interactions are guaranteed (Axelrod and Hamilton 1981; Trivers 1971). This may apply in the case of ravens, although it is also the case that groups are relatively fluid and change membership regularly. What is needed here is data on the probability of repeated interaction and the benefits and costs of communicating.

11.4 From mechanism to function

We have emphasized synergy as an important explanation of the evolution of co-operative signaling in animal groups. While most evolutionary biologists are on some level aware that synergy can play a role in the evolution of co-operation between large numbers of unrelated individuals, it is seldom stressed when considering social communication. For example, much of the work on **central place foraging** starts from the view that signaling about food cannot evolve unless there is always a direct benefit, such as anti-predator vigilance, from travelling to food in groups (Dall 2002; Richner and Heeb 1996). The argument is that if there is not a direct benefit to costly signaling then a 'do nothing' strategy can invade the population. In terms of the model in Table 11.1, in order for communication to evolve we must have $D>C$. In this case, a single mutant co-operator can invade a population of defectors.

While the 'direct benefits' argument is correct, it can obscure the fact that co-operation can still evolve even when there is no direct benefit to co-operation for a mutant in a population of defectors, i.e. $D<C$. In terms of two player games this is when $E>C$ and there is some form of extra or synergistic benefit to co-operation. In the model in Box 11.2, costly communication can be an evolutionarily stable strategy provided that per capita productivity increases at least linearly with group size. In this case, 'do nothing' will not benefit from failing to communicate because their breaking the communication link will lead to a decrease in success not only for other group members but also for themselves. As more individuals participate in communication the greater their effectiveness of the groups' actions. Such an argument gives a strong justification for the information centre hypothesis for central place foraging first proposed by Zahavi (1971).

Synergy has important consequences for how we conduct experiments to test the evolution of co-operation. West *et al* (2006) propose that a first step are experiments looking at growth rates of isolated groups of 'communicator' or 'do nothing' individuals with growth rates of mixtures of the two types. Consider two such experiments we might perform on bacteria or animal groups. The first experiment establishes that a 'do nothing' mutant can invade a resident population of communicating individuals. In a second experiment a 'communicate' mutant is shown to be unable to invade a population of 'do nothing' residents due to a cost of signalling. The second of these experiments is similar to the that performed by Diggle *et al* (in press) and discussed in Chapter 2 of this book. They found that non-signaling bacteria grow faster in nutrient rich environments than signaling wild types and that mutant non-signalers invade a population of signalers.

Should we necessarily conclude from our hypothetical experimental results that the evolution of costly signaling requires some form of inclusive fitness benefit? The answer is 'no'. To see this, consider the selective pressure in each of these experiments with relation to Figure 11.5, for group sizes slightly larger than that at which all cooperate is a stable strategy. Here there is a stable state corresponding to a mixture of co-operators and defectors, as well as a stable state corresponding to all defect. The results of these experiments are consistent with this model: communication can be selected against in very large populations of 'do nothing' individuals and communication is also selected against in a large population of communicators. However, at an intermediate group size where a substantial number of individuals are already co-operating the selective pressure is for increased and ultimately full co-operation. In such a situation there is no need to invoke inclusive fitness to justify communication. Costly signaling can evolve between non-relatives, although non-signalling individuals will remain when group sizes become very large.

The difficulties arising in interpreting experiments illustrates the intimate connection between mechanisms and function. Without knowing the mechanism of communication and how they depend upon the number of interacting individuals we cannot predict whether or not a particular form of communication will evolve. The prediction of the model in Box 11.2 depends crucially upon the non-linear shape of the benefit function. It is important therefore to measure this benefit function in a wide range of contexts. This has been done in some of the studies of social foraging that we have reviewed here. A number of studies of nest establishment by insects have also shown that per capita success increases with group size. Further work is needed to link together mechanisms, of for example, costly signaling chemicals with growth of bacteria populations. Establishing the form of group benefit functions will help demystify the wealth of co-operative interactions seen at all levels of biological organization.

Summary

Synergy is where the interactions of a group of individuals becomes more than the sum of their parts. In this chapter we review how, through the use of social communication, foraging animals can increase their rate of finding food. We discuss how mechanisms such as pheromone trails, dancing and other signals act to increase group, and thus individual, success. We also discuss how social dilemmas can arise where costly signalling can be exploited by non-signallers. We show that under a range of conditions, specifically when group success increases more than linearly with group size, co-operative signalling can evolve without kin selection or reciprocity. This study serves to emphasise the importance in linking mechanism with function when studying collective behaviour of animals.

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