Chapter **20**

Signal Honesty

THE PRIOR CHAPTER BROACHED THE POSSIBILITY that sender and receiver may have conflicting interests in the accurate exchange of information. This is rather different from the happy collaboration assumed in Part II. When might we find discordant expectations between communicating animals? Consider the opponents in an aggressive encounter over some resource. Each performs threat displays to persuade the other to retreat without engaging in an escalated battle. Successful persuasion avoids the risk of injury, but whoever retreats fails to gain the resource. There is thus a conflict of interest. Alternatively, consider a courting pair in which the male benefits by mating regardless of his suitability, whereas the female prefers to mate only if the male meets certain criteria. Suppose the major information available to females is that signaled by the body ornamentation or displays of male suitors. Males and females are unlikely to have similar enthusiasm for reliable signaling. Finally, consider a hungry cheetah stalking a gazelle. If the gazelle can perform a display indicating that it is too agile to be worth chasing, perhaps the cheetah will give up the hunt. But

should a less agile gazelle be honest about its greater vulnerability? In each of these cases, at least some senders will be tempted to provide false information. Receivers subject to such false signals will do best to discount or ignore them. How the corresponding evolutionary game will play out has been a major preoccupation of researchers in animal communication. The history of views on this topic is itself instructive and we shall briefly review it below. First, however, we need to refine our definition of honest communication.

HONESTY VERSUS CHEATING IN COMMUNICATION

The opposite of honesty is cheating. In a communication system, senders might cheat on receivers, and receivers might cheat on senders. In Chapter 12, we called the first form of cheating **deceit**. There are several ways in which a sender might deceive a receiver. One type of deceit occurs when the condition that is important to the receiver has only a few discrete and unordered alternatives, and the sender emits a signal that falsely identifies which alternative is true. For example, young males in lek mating species may mimic the patterning or behaviors of females to avoid harassment by older males and sneak closer to receptive females. Another example is a bird that gives a false alarm call, causing competing foragers to flee and leave any food to the caller. Hasson (1994) calls such false categorical signals **lies**. A special case occurs when a sender **witholds** production of a signal that could benefit a nearby receiver. A bird in a foraging flock might refuse to give an alarm when a hawk or snake is spotted, or a lone monkey might fail to produce recruitment calls when it discovers a rich patch of fallen fruit. By witholding the signal, the sender is falsely implying that one of two alternative conditions is the case. Deceit can also occur when the alternative conditions that receivers seek to identify are from a continuous set and reflect the value of some single property. Typically, the communication code maps each possible signal on a subset of the ranked values of the property. A sender may cheat by exaggerating or bluffing about which value of the property is currently true. One of two opponent dogs might growl more loudly at another than is justified by its willingness to fight. Its signal is thus a **bluff** or **exaggeration**. Finally, we discussed the possible role of amplifiers in Chapter 12. These are traits that make the direct assessment by a receiver of some property in a sender simpler or more accurate. The cheating version of an amplifier is an **attenuator**. This is a trait that makes direct receiver assessment of the sender property more difficult (Hasson 1994). An example is broken and patchy body marking on a fish that hinders the estimation of its body size by conspecifics.

In each case, naive acceptance of the dishonest signal (or absence of a relevant signal) can cause the receiver to select a subsequent action that is worse for it than the alternatives. Although this might enhance the value of information for the sender, it will reduce the value of information for the receiver. From its own point of view, the receiver has been induced to err as a result of reliance on the cheating signal. Deceit thus implies receiver error. It is important to note that the reverse is not necessarily true and receiver error is not a

useful indication of deceit (Dawkins 1993; Dawkins and Guilford 1991; Wiley 1994). We saw in Chapter 14 that imperfect signals always lead to errors that a receiver without reliance on signals would not make. These errors are one of the incidental costs of communication. We also saw that it is rarely optimal for a sender to transmit and a receiver to demand perfect information; the costs usually outweigh the benefits. As a result, receiver error is nearly always a part of optimal communication strategies; how much error is tolerated will depend on phylogenetic and physiological limits on signal design, the costs of encoding and decoding signals, effects of the propagation medium, the relative benefits to both parties of reliable signaling, and the decision rules utilized by receivers. Whereas receiver error occurs in both honest and dishonest communication, both parties enjoy a positive value of information only when the signal is honest.

The alternative form of cheating is **exploitation of a sender** by a receiver. A sender sends honest information, but the subsequent decision made by the receiver is one that benefits itself at the expense of the sender. Here the value of information is negative for the sender, but positive for the receiver. Again, the best indicator of cheating is a difference in the sign of the values of information for the two parties.

A BRIEF HISTORY OF HONEST SIGNALING

Early ethological studies of communication focused on the evolutionary origins of signals. As we discussed in Chapter 16, many signals appear to have evolved through the ritualization of behaviors that are or were functionally appropriate to the contexts in which signals are now used. Erection of feathers or fur during agonistic conflicts can have tactical advantages if an animal is likely to be pecked or bitten. Not surprisingly, fur and feather fluffing has been incorporated into many agonistic signals. A bird uncertain whether to attack or flee may vacillate, and the resulting mixture of motor patterns can be ritualized to become a display. If this is the general mechanism by which signals evolve, it is logical to conclude that the actions performed in displays will be accurate indicators of underlying motivations. Put simply, many early ethological studies presumed that most signals were honest because the sources of signals were physiologically or anatomically linked to the motivations of the sender (Cullen 1966; Moynihan 1970; Smith 1977).

With the rise of evolutionary game theory in the 1970s, students of animal communication became more skeptical and even cynical about the honesty of animal signals. If a sender wears its heart on its coatsleeve, what prevents a clever receiver from using this information to exploit the sender? Is it really optimal to announce the limits of one's true willingness to fight at the onset of an agonistic encounter? Should a gazelle try to perform an agility display to an approaching cheetah when it is not agile enough to escape an actual chase? If two animals are engaged in a war-of-attrition contest, should either party announce how long it intends to display? Such a declaration would surely allow the opponent to select a longer display time and thus win.

Dawkins and Krebs (1978; Krebs and Dawkins 1984) went even further. They suggested that senders are likely to be deceitful manipulators, trying to mask their true intentions and trick receivers into actions benefiting the sender; receivers should be mind-readers trying to discount false signals, anticipate the true intent of the sender, and thus identify their own best counter-move. The result is a never-ending arms race in which increased deceit and concealment of true intentions by senders is parried by increased discrimination and more efficient exploitation by receivers. Except where sender and receiver have common interests, senders should never reveal their true intentions, and so signals would largely be deceitful or uninformative.

This view was countered by Zahavi (1977a, 1980, 1987, 1993, 1997). He argued that receivers ought not respond to signals unless they were honest. If a receiver does not respond to a signal, then there is no selection on senders to provide one. Receivers should thus have the upper hand in any arms race. Given this control, the optimal strategy for a receiver would be to respond only to those signals that carry some guarantee of honesty. One way to do this is to require that signals impose a cost such that the sender could not afford to produce the signal, or would produce it in an ineffective manner, were the provided information untrue. Zahavi called such costly signals **handicaps**. For example, suppose two dogs threaten each other. In principle, threats could be symbolized by any doggy sound. However, dogs, like most vertebrates, favor harsh, low-frequency sounds as threats and higher pure tonal frequencies to indicate submission (Morton 1977). As we have seen, body size limits the lowest frequencies that a sender can emit at a reasonable amplitude. Thus, insisting on low-frequency threat sounds allows for honest assessment of relative body sizes and assessment of whether further escalation is a good idea or not. Zahavi (1987) added that it may be more difficult to produce a low-frequency sound than a high-frequency one when the vocalizer is tense and prepared to flee. A dog that is confident it would win an escalated fight can afford to relax enough to produce a low frequency, whereas the production of a low-frequency sound by a tense and unsure animal might either be physically impossible or require the relaxation of muscles that should be kept tense in preparation for flight. By insisting on a signal that is reliably linked to the true motivation of the sender, the receiver is thus able to guarantee honest information. As a second example, consider a female bird that wants to mate with the most proficient forager she can locate. One way to compare males is to require each to bring her multiple samples of favored prey. Many birds do just this. Finally, consider a cheetah approaching a gazelle. A display of agility by the gazelle will surely attract the attention of the cheetah to it rather than to alternative prey. Only a truly agile gazelle can hope that the risk of increased conspicuousness will be outweighed by the persuasiveness of its performance. Some other possible handicap signals are shown in Figure 20.1.

What about displays that are highly stereotyped? Doesn't such stereotypy preclude the extraction of honest information about the sender? The classical explanation for stereotypy is that there is an optimal signal form that minimizes distortion during propagation between sender and receiver (pages 461–462). Zahavi proposed an alternative explanation. He argued that stereo-

(A)

(B)
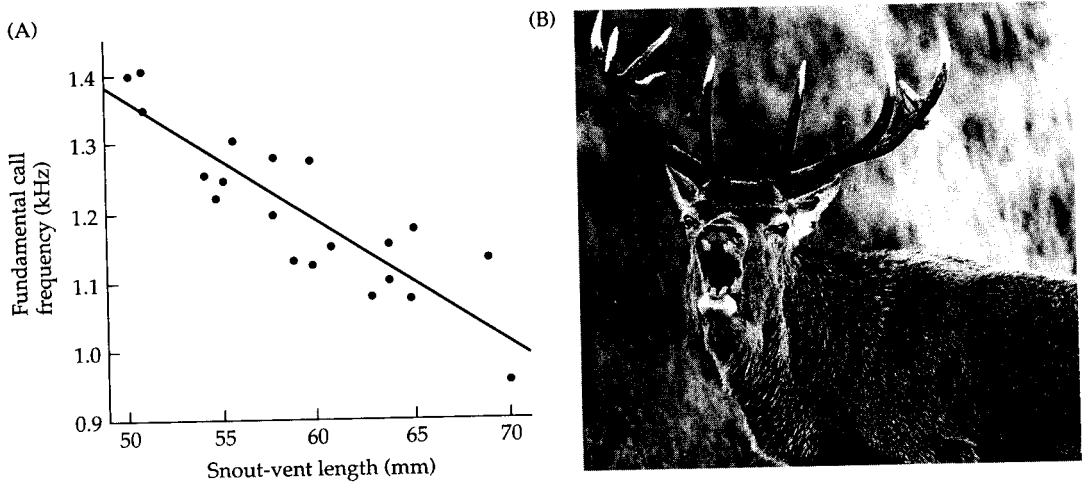
Figure 20.1 Some possible examples of handicap signaling as suggested by Zahavi. (A) Deep croaks in toads. Some workers have suggested that producing a deep frequency call is an uncheatable and honest indicator of male body size. This plot shows the relationship between male body size (as measured by snout to vent length), and the fundamental frequency of 20 male toads' calls. Only larger toads can produce lower fundamental frequencies in their calls. (B) Roaring by male red deer. Stags compete vigorously for females each fall. Before fighting, competing males will often roar at each other. This is an expensive behavior that mimics the use of many muscles and behaviors actually invoked during fighting. It is thought that only those males in good enough condition to fight can produce roaring at a winning level (Clutton-Brock and Albon, 1979). (A after Davies and Halliday 1978; B courtesy of Tim Clutton-Brock.)

typed displays are used by receivers to compare important qualities in senders that are not easily measured by direct assessment. A clever receiver would require that each sender perform a display according to some difficult standard—only those of the highest quality could perform the display with a close fit to the ideal protocol. The result would be a high degree of stereotypy, but just enough remaining variation to assay sender qualities.

Zahavi's suggestions were initially received with considerable scepticism. One reason is that he did not specify formal evolutionary models for how handicaps might evolve, but instead gave many examples that could be plausibly interpreted as handicaps. Different examples on these lists relied on different handicap mechanisms. The earliest attempts to model handicap evolution focused on mechanisms that turn out to be difficult to establish evolutionarily (Maynard Smith 1976b). Some concurrent surveys of displays used in agonistic contexts concluded that signals were rarely honest indicators of the sender's next actions (Caryl 1979; Paton and Caryl 1986). These initial doubts have been succeeded by alternative game-theoretical models that demonstrate the evolutionary plausibility of handicap signaling and verify the need for a costly guarantee if signals are to be honest. The result has been a wider acceptance of Zahavi's principle. In addition, refinements in the methods for assessing sender honesty have resulted in increasing numbers of

field and lab studies supporting moderately honest signaling by senders. In the following section, we shall examine some of these more recent models briefly, identify the kinds of traits that might constitute suitable handicaps for each context, and review evidence for and against honesty in animal communication.

GAME MODELS OF SIGNALING INVOKING HANDICAPS

It is unlikely that there is a single communication game for all situations. In Chapter 12, we classified communication exchanges according to the contexts in which the exchanges occur. As we demonstrate in subsequent chapters, these contextual categories differ markedly in the degree to which sender and receiver share common interests, the degree to which a sender might be tempted to deceive the receiver, and the selective forces on the receiver to demand guarantees of honesty. This means that different game-theoretical models may be needed for different contextual categories of signaling.

Within each contextual category, the relevant game may also depend upon the degree to which the information sought by the receiver is provided by signals. As discussed in Chapter 12, a receiver has potential access to as many as four sources of information about any given set of contingencies: prior probabilities of occurrence, direct assessment by the receiver unaided by a sender, direct assessment by a receiver enhanced by amplifier traits, and coded information in sender signals. In any given situation, the relative emphasis on each source of information will vary. The degree to which information sources other than signals are available to verify or test sender veracity would seem to be important in the type of evolutionary game considered. Similarly, the sender has the option of trying to force a receiver to act a certain way (e.g., through tactical behaviors, page 355), combining some elements of force with signals, or just providing signals. The relative weighting of tactical versus signaling components in an exchange may also affect the kind of game modeled.

The nature of the handicap costs will also affect game propriety. We distinguished between two kinds of costs on pages 538–544. **Necessary costs** are intrinsic to communication and are independent of receiver responses. Both parties suffer necessary costs, but it is the necessary costs inflicted on senders that affect signal honesty. **Incidental costs** arise because imperfect signals generate errors in receiver decisions, or because payoff matrices change when signaling is adopted. Only the latter changes are likely to affect senders. The two types of costs guarantee honesty in somewhat different ways. The former are usually experienced before or during signal production. To be handicaps, they thus must be physically linked in some way to the information sought by the receiver. For example, we have noted many times that a small animal will have difficulty using a dipole source to produce low-frequency sounds. In some cases, it might be able to do so, but the requisite energy outlay would surely exceed the benefits. If low-frequency codes for body size, honesty is guaranteed by physical laws and the necessary costs of signal production. The most common incidental cost enforcing honesty is punishment. Consider a

solitary monkey that discovers a patch of fruit. It will get more food if no other monkey elects to feed with it. However, if discoverers are expected to advertise their food finds with signals, the discoverer may have a higher payoff by sharing than by being punished when found not sharing. The payoff matrix for the sender is thus different depending upon whether advertisement signals are expected by dominant receivers or not. If the average amount of food consumed by a subordinate monkey declines when signals are produced, there is thus an incidental cost to their giving these signals. Punishment may be a powerful and widespread deterrent to deceit in animal societies (Clutton-Brock and Parker 1995a).

As Dawkins (1993) and Guilford and Dawkins (1995) point out, a reliance on necessary costs to ensure honesty will limit suitable signal forms. This in turn constrains signal optimization for efficient coding, minimal distortion during transmission, and maximal detectability and discriminability by receivers. Where honesty is largely ensured by incidental costs such as punishment, a much wider range of signal forms can be used, and this will affect both the amount of information provided and the values of information for both sender and receiver. The type of honesty-enforcing cost demanded by receivers thus has major repercussions on subsequent evolution of the signal exchange at both the game-theoretical and simple optimality levels.

We now turn to some of the more instructive game-theoretical treatments of honest signaling. These vary in the contextual categories of information provided, the availability of alternative sources of information, and whether costs are necessary or incidental. As a guide, the games are summarized in Table 20.2 (page 669). Despite the variation in game structure and assumptions, we shall see that the basic take-home message of the models is remarkably similar.

Honesty and Agonistic Signals

Consider two equally matched opponents that both seek the same resource. They differ in the value that they place on this commodity. For example, the same item of food might be much more important to a starving animal than to a sated one. Should they end up fighting, it is likely that the animal that values the resource the most will fight harder and/or longer and thus win. It might seem optimal for each party to signal their perceived value of the resource at the outset. This signal would lead to the same outcome as if they had the fight but without all the risks and costs. However, this peaceful strategy could be easily invaded by a cheat that always signaled a very high valuation. Are there any conditions when it would still pay to provide an honest signal?

One version of this game has been examined by Enquist and colleagues (Enquist et al. 1985). In this model, information about valuation is provided by the sender through its choice of alternative actions. These could be pure displays or they could be a mixture of display and tactical actions. Relevant sender costs could be necessary, incidental, or some mixture of the two. Available sender options will vary in the degree to which they inflict such costs. For example, a display close to an opponent is much more risky than one performed at a distance. At the same time, displays are likely to vary in their ef-

Table 20.1 Cost, effectiveness, and honesty of agonistic displays of American goldfinches (*Carduelis tristis*) during conflicts over access to seeds at a bird feeder

Sender display[a]	Receiver responses (%)[b]				
	LF	HHF	WF	Attack	Retreat
LHF	15.5	24.1	60.3	0	0
HHF	3.8	7.6	74.7	2.5	11.4
WF	0	0.2	48.8	31.1	19.9

Sender display[a]	Sender's next act (%)[c]				
	LF	HHF	WF	Attack	Retreat	Win
LHF	0	12.1	67.2	5.2	15.5	0
HHF	0	2.5	62.0	13.9	10.1	11.4
WF	0	0	11.1	19.7	40.3	28.9

[a]There are three main displays: low-intensity head forward (LHF) in which displayer faces opponent with neck partially extended; high-intensity head forward (HHF) with the next further extended, head lowered, and partially open bill pointed at opponent; and wing flap (WF), similar to the HHF with the addition of raised and spread wings.

[b]The percentage of receiver responses to each sender display. Using the probability that a receiver will subsequently retreat as an index of display effectiveness, the three displays can be ranked as LHF < HHF < WF. Similarly, if the cost of each display is the chance that it will elicit an attack by the receiver, the displays can again be ranked in the order LHF < HHF < WF. If the receiver responds by displaying, it usually selects a more effective display and thus increases the risk to the sender. Thus, as predicted by Enquist et al. (1985), display effectiveness and cost are positively correlated.

[c]The next act performed by senders after giving each type of display. Senders giving a higher-intensity display were more likely to follow the display with attack; if the next act of the sender was a display, it was never a less-effective display and, where possible, usually a more effective one. Both suggest that the sender's choice of display is an honest indicator of its intentions. The probability of subsequent sender retreat increases only for WF displays, an effect often due to loss of the contest by the sender (Popp 1987).

fectiveness. For example, a loud growl accompanied by a swipe with bared claws may partly disable an opponent, whereas a snort from a distance will do little to alter the outcome of a fight. Let $-C_i$ be the average cost to the sender of display i (including both the costs of performance and any increases in the risk of subsequent injury), P_i the probability of winning the interaction if this display is used (e.g. the effectiveness), and V the perceived value of winning the contest from the point of view of the animal choosing which display to perform. The average payoff of performing any given display is thus $\overline{PO}(i) = P_i V - C_i$. If we plot the average payoff for any display i against various values of V, we shall obtain a straight line with a slope equal to P_i and an intercept on the ordinate of $-C_i$. All such display lines will have a positive slope; however, displays with higher effectiveness will have steeper slopes, and those with higher costs will have a lower intercept.

It seems most likely that the higher the effectiveness of a display (hence the steeper its slope), the higher the cost of that display to the sender. In Figure 20.2, Displays 3 and 4 show this type of positive correlation between effec-

tiveness and cost. Display 3 is more effective, but its higher cost causes it to begin lower down on the ordinate axis. The result is that the two lines cross at some point. For V values greater than that at the crossing point, the sender gets a higher payoff by choosing to perform Display 3; for lower V values, it should perform Display 4. Its choice of a display will thus be an honest indicator of how much it values the resource and hence how much it would be willing to fight an escalated battle. Put another way, a positive correlation between signal effectiveness and the absolute value of costs leads to honest signals. What about the converse? Does honest signaling require a positive correlation between signal costs and effectiveness? Figure 20.2 shows lines for two other displays for which effectiveness and costs are negatively correlated. Display 1 has higher effectiveness than Display 2, but it has a lower cost. In this
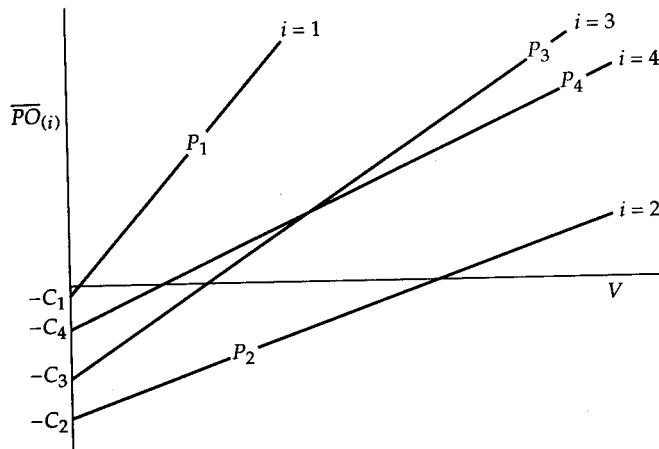
Figure 20.2 Enquist and colleagues' (1985) model for honest signaling by choice of display in agonistic encounters. This model assumes that each player can choose any of several displays or actions. These displays differ in the cost ($-C_i$) to the sender of producing display i, and in the display's effectiveness, characterized here by the probability (P_i) that using that its performance will lead to winning the contest. For any perceived value (V) of the prize to be won, the average payoff of using display i is $\overline{PO}(i) = P_iV - C_i$. The lines in this example show the average payoff values as V varies for four different displays. If Display 1 is an option, it is clearly the best, as it yields the highest average payoff for any V. This is because it has a very high value of P_i (which determines the slope of the payoff line) and a very small value of C_i (leading to a high intercept of the payoff line with the ordinate axis). Similarly, the animal should never use Display 2, as it always has the lowest payoff as a result of a small P_i and large C_i. As a rule, one expects higher effectiveness to require higher costs. This type of pattern is shown with Displays 3 and 4. Although the higher cost suffered by performing Display 3 instead of Display 4 leads to lower payoffs at low values of V, the lines cross as V is increased, and at higher V values, the steeper slope of the Display 3 line eventually makes it the better option. The optimal animal will use Display 4 if it does not value the prize highly, but will choose Display 3 if it has a high valuation of the prize. Where display effectiveness and cost are positively correlated (as with Displays 3 and 4), an animal's choice of behavior will be an honest indication to its opponent of its motivation and subsequent willingness to fight.

case, the optimal choice is to use the same option (Display 1) regardless of perceived V value. Signaling here provides no information about sender motivation. At least in this model of agonistic contests, honest signaling is likely only if costs and effectiveness are positively correlated. A more formal analysis of this evolutionary game is given by Enquist (1985).

The model thus supports Zahavi's handicap notion. Sender costs are necessary for honest signaling, and if these costs have the right relationship to benefits to make cheating uneconomical, honest signaling is the ESS outcome. What evidence is there that display costs and effectiveness are positively correlated in real agonistic contests? Popp (1987) focused on precisely this question using aggressive interactions between goldfinches at bird feeders during the winter. The results show a clear correlation between the risks of subsequent attack and the effectiveness of different displays (Table 20.2). In addition, as the value of the resource increased (either because of decreased food or increased needs due to low temperatures), birds were more likely to adopt the riskier displays. These results fit the Enquist et al. (1985) model nicely. Several other studies also show support for honest agonistic signaling when costs and effectiveness are positively correlated (Andersson 1976; Enquist et al. 1985; Hansen 1986; Nelson 1984; Waas 1991a,b). One reason these studies contradict the earlier reviews of Caryl (1979) and Paton and Caryl (1986) may be the better controls for complex sequential interactions in the more recent papers (see pages 704–706).

Honesty and Courtship

Mate choice was the original context that spurred Zahavi (1975) to develop his handicap principle. In the typical scenario, females seek to choose mates based on some male quality that is difficult to assess directly. Females might seek males that are good foragers, those with superior immune systems, those most able to protect a female against harassment, and so on. This choice could lead to direct benefits for the female's survival and/or fecundity, or to indirect benefits through the acquisition of good genes for her offspring. Because the quality of interest is hard for females to assess directly, males that honestly signaled their quality value would greatly facilitate female choice. In species where females have the upper hand in mate selection, there would thus be strong selection favoring males that produced honest signals. However, the usual problem arises: Why should lower-quality males produce honest signals?

Grafen (1990a,b) modeled this communication game as a continuous, asymmetric scramble. In his model, males vary continuously in the quality females wish to assess. Males can also differ continuously in at least one parameter of the courtship display that they perform to females. For example, the variable parameter might be display intensity. Alternative male strategies differ according to the function by which the variable display parameter codes for sender quality. Males adopting an uninformative strategy display at the same intensity regardless of their quality values; males adopting an informative and honest strategy adjust the intensity of their display to reflect their relative quality. Females in this model observe courting males and use their perceived differences in male display to infer relative male qualities. Female

strategies differ in the function by which they translate these perceived display differences into estimates of male quality. Thus females adopting a sceptical strategy might treat all display intensities the same. That is, they would ignore any signal information. Others might use a strategy in which the ranks of perceived display intensities were used to estimate the quality ranks of males. Male fitness in this model depends upon (A) the true quality value of that male, (B) the necessary costs it pays to perform its display, and (C) the degree to which females infer from its signals that one male has a higher quality than other males. Note that this last emphasis on relative inferred quality makes this game a scramble because the payoff for any one male depends on what other males are doing and how they are perceived. Female fitness in the model is assumed to be maximal when female estimates of male quality are closest to true male quality. The more accurately females assess males, the higher their fitness. Clearly this game is asymmetric with different available strategies and different payoffs for the two roles (here, the two sexes).

This is a difficult game to solve. With some reasonable assumptions and simplifications, Grafen showed that there are two ESSs: (a) males do not display honestly, and females ignore all signals; and (b) all or most males are honest, and all or most females attend to signals. The latter ESS can occur if and only if four specific conditions are met. These are illustrated in Figure 20.3. One condition follows directly from the assumptions of the model. It must be the case that the higher the perceived quality of a male, the more likely females are to mate with him. That is the whole point of female assessment in the first place. A second condition for the ESS, and one that supports Zahavi's general principle, is that signaling must be costly to male senders. If we ignore subsequent reproductive benefits, a male's fitness must decrease as a result of performing the signal. The third condition is the one that actually guarantees honesty: a given investment in display must cost a high-quality male less than that same display investment would cost a poor-quality male. How does this ensure honesty? Male mating success depends upon which male displays at the highest intensity. This could lead to an arms race in which successive males increased their display effort until they were just ahead of the competition. The resulting escalation would lead to higher and higher mean costs of display. Note that the number of females waiting to mate remains constant. Thus the benefits of being top male would not change, whereas the costs keep going up. Eventually, costs would exceed benefits and no further escalation would be favored. The third condition in Grafen's model thus states that the break-even point halting escalation will occur at a lower total cost for low-quality males than for high-quality ones. The fourth and final condition requires that low- and high-quality males who are perceived to have the same quality (either due to female error or to higher display investment by the low-quality male) are treated the same as potential mates by females. This ensures that the higher costs that low-quality males pay to display at a given level are not more than made up by special treatment from females later on.

Mate choice is one driving force in **sexual selection**. This is the process Darwin invoked to explain why members of the sex in greatest competition for mates (usually males) should exhibit traits that so often reduce their via-
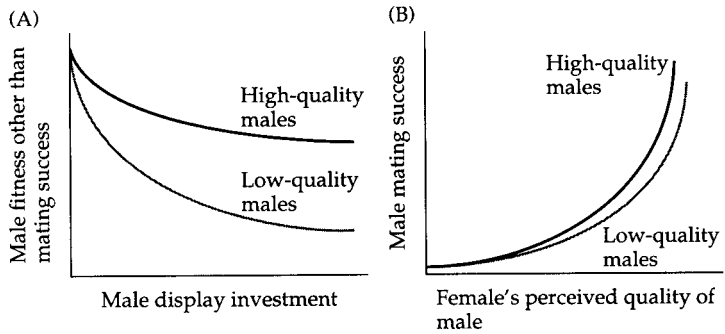
Figure 20.3   Four basic conditions required for honest courtship signaling to be an ESS. (A) Male fitness, holding the effects of mating success fixed, must decrease as male display investment increases. Thus both lines in this plot decrease as display investment increases. This simply means that signaling has to impose a fitness cost on the senders. The second condition is that, for any given investment in display, the fitness costs must be less for high-quality males than for low-quality ones. Thus the fitness curve in the plot for low-quality males must always lie below that of high-quality ones. (B) A third condition is that the higher in quality that females perceive a male to be, the more likely he is to mate. This is the starting point for the entire game, namely that females prefer to mate with high-quality males. Finally, the rate at which male mating success increases with female perception of their quality must be no higher for low-quality males than for high-quality ones. Put another way, low-quality males are treated the same or worse by females when perceived as having the same quality (albeit erroneously) as high-quality males. (After Grafen 1990a,b.)

bility. As we shall discuss in detail in Chapter 23, sexual selection must be, at least in part, a genetic process. Grafen's models of courtship signal evolution explicitly exclude some of these genetic processes. However, his goal was to show that even without special genetic processes, courtship signals could evolve as long as they were handicaps. A variety of genetic models can also explain the evolution of such signals, and it is reassuring that these predict the evolution of costly courtship signals only if low- and high-quality males differ in their ability to produce the signals (Andersson 1994; Iwasa and Pomiankowski 1991). Despite very different assumptions, the game-theoretical and genetic models have largely led to similar conclusions about the necessity for handicap costs in signal evolution.

Testing the handicap principle in male advertisement signals has proved challenging. Where the benefits to females of choosing a male affect their fecundity or survival directly, the qualities that females seek can often be identified and predictions tested. Where the benefits are paternal traits inherited by offspring, the task is more difficult. Despite the difficulties, there are increasing numbers of studies supporting honest handicap signaling during courtship. For example, Knapp and Kovach (1991) showed that the display rates of male damselfish were an accurate indicator of the abilities of males to tend the eggs laid for them by females (Figure 20.4). Females would benefit directly by selecting male mates with high rates of display, and this is in fact

(A)

(B)

Male display rate (dips/10 min)

(C)

Male display rate (dips/10 min)
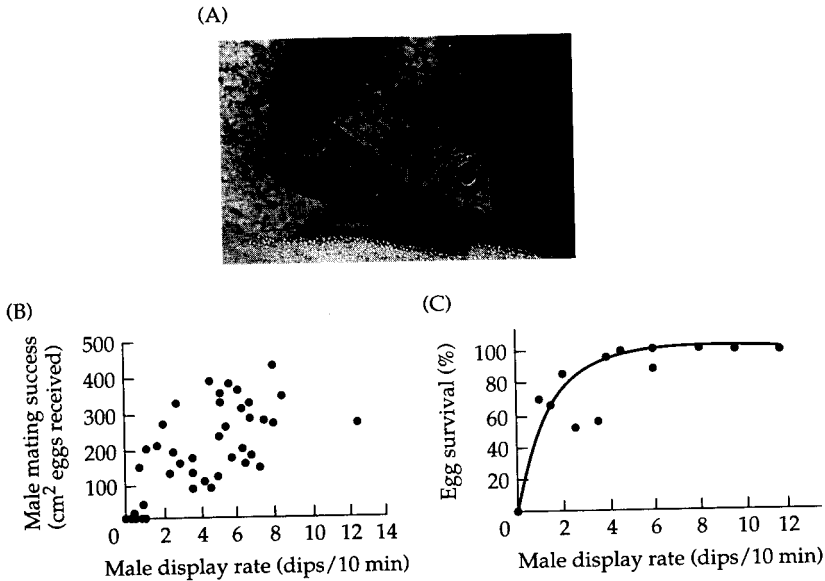
Figure 20.4 Honest courtship displays by male damselfish (*Stegastes partitus*). (A) Male damselfish tending the mass of eggs laid for it by the females with which it mated. (B) Male damselfish mating success, measured as number of eggs laid in the territory, versus male display rate measured as dips/min. Males with higher rates of display attract more females and thus obtain more fertilized eggs to tend ($r = 0.85$; $p < 0.0001$, $N = 48$). (C) Egg survival as a function of male display rate. Males with higher display rates are better parents. (A courtesy of Ken Clifton; B and C after Knapp and Kovach 1991.)

what is observed. Display rate is an honest but costly indicator of male paternal ability that is used by female receivers to select mates. Another example is the use by displaying males of red or orange carotenoid pigments in their plumage, skin, or scales (see page 549). No vertebrate can synthesize carotenoid pigments; they can only be acquired by foraging, and different levels of coloration should be honest indicators of male foraging abilities. In guppies and house finches, this appears to be the case; the better the male as a forager of sources of carotenoid pigments, the redder his coloration (Endler 1980, 1983; Hill 1991, 1994; Kodric-Brown, 1989). Females in these species appear to rely, at least in part, on male coloration in the selection of mates (Figure 20.5; Milinski and Bakker 1990). We shall take up other examples of honest courtship signaling in Chapter 23.

One final comment about Grafen's model. Because he explicitly excluded genetic processes peculiar to sexual selection, his model can be applied to any kind of signaling game in which a sceptical receiver must deal with a possibly devious sender. Grafen has thus provided the closest thing to a general communication game that we shall discuss in this chapter.
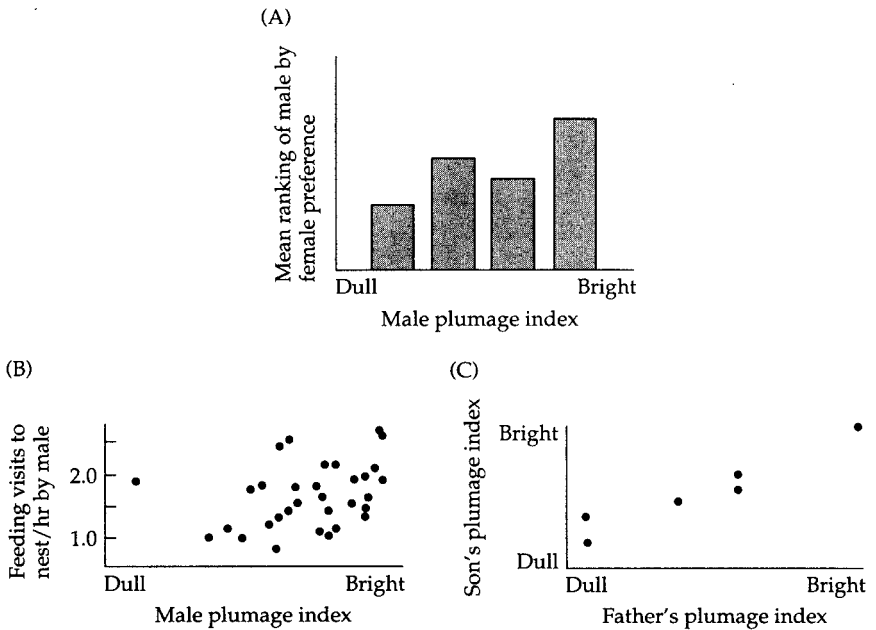
Figure 20.5 Female choice of mate and carotenoid colors of male house finches (*Carpodacus mexicanus*). House finch males vary in levels of carotenoid pigments in their feathers. Some are yellow and have little coloration (dull plumage index), whereas others have lots of conspicuous red coloration (bright plumage index). (A) Captive females offered proximity to four males of different plumage indices show significant preferences for brighter males ($p < 0.05$; $N = 14$). (B) The number of feeding trips made to the nest by wild male house finches is higher for brighter plumaged males ($r_s = 0.63$; $p < 0.05$; $N = 13$). Male coloration may thus be an honest indicator of male paternal qualities. (C) Females may also benefit by mating with bright males because they are likely to father sons who will themselves have bright plumage, be preferred by females, and thus be successful. Plot shows correlation between father plumage index and that of sons ($r_s = 0.91$; $p < 0.01$; $N = 6$; only one son from each nest was included to preserve independence of points). (After Hill 1990, 1991.)

Honesty and Badges of Status

Once animals that are capable of individual recognition have fought each other, it may pay to avoid escalation in future encounters because the outcome would be largely predictable. Even without individual recognition, if individuals that frequently won escalated contests exhibited some **badge** reflecting their currently dominant status, this might save all parties from unnecessary risk and injury (Rohwer 1975, 1982). One apparent example is shown in Figure 20.6. As discussed on pages 637–640, it often pays animals to adopt submissive behaviors when their chances of winning an escalated fight or the ratio of benefits to costs is low. Wearing or not wearing a badge makes observance of such status roles easier. But as with agonistic and courtship signals, one cannot help wondering what would prevent a sender from cheating by sporting a badge exaggerating its prior contest success or its willingness to fight if challenged.

(A)

(B)
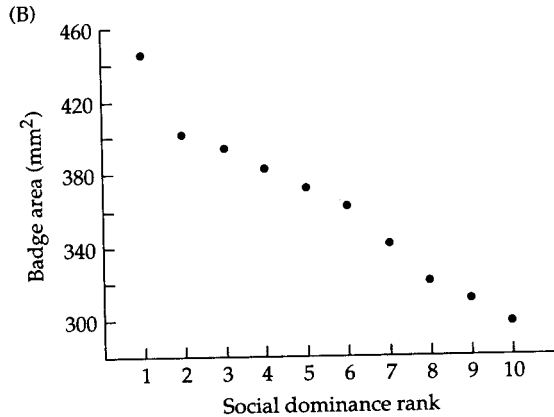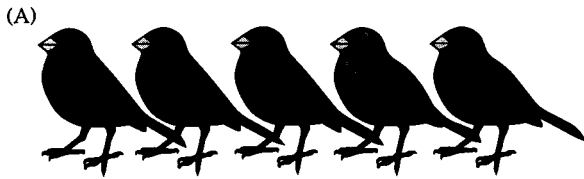
Figure 20.6   **Badges of status in male house sparrows** (*Passer domesticus*). (A) Variation in badge size among adult males. (B) Plot of male badge area versus social dominance rank in one flock of house sparrows captured in Denmark. Smaller numbers on the abscissa mean higher dominance rank. (After Møller 1987a,b.)

Maynard Smith and Harper (1988) modeled one badge-of-status game. They noted that badges in many species are better correlated with aggressive motivation than with fighting ability (although the two may be linked to some degree). They therefore considered a continuous symmetric contest in which players select both level of aggressiveness and size of status badges. Honest signaling would consist of a stable mixture of aggressive animals with large badges and nonaggressive ones with small badges. They found that such an honest mixture was an ESS only if the costs of escalated fights, relative to the benefits of winning, increased rapidly with increasing badge size, and animals with large badges were often challenged by others with large badges. Cheating would be disadvantageous because sporting large badges but lacking the corresponding motivation to win would be very dangerous. Again, we find that honesty exists only if there are signaling costs that are most felt by deceitful senders. As with the dominance game discussed in the prior chapter, honest signaling and observance of status ranks is favored only when the benefit to cost ratios or the chances of winning are sufficiently low; when either or both are high, even less aggressive players should ignore the signals and escalate.

The situation is a bit more complicated than this model implies because it is possible to identify additional mutant strategies that can invade a mixture of honest badges. For example, several studies have considered a cryptic aggressor strategy in which a very aggressive animal exhibits a small badge. In Owens and Hartley's (1991) version, this "Trojan sparrow" is nonaggressive when contested resources are abundant, but exhibits its true aggressiveness when they are scarce. Johnstone and Norris (1993) examined a small-badged

mutant that is never challenged and attacked by animals with large badges, but itself attacks and wins fights with less aggressive small-badged individuals. Either of these mutants would invade and destabilize the honest ESS mixture described by Maynard Smith and Harper. However, Johnstone and Norris have also shown that if there is a common cost to being aggressive, whether one engages in escalated fights or not, cryptic aggressors cannot invade and the honest mixture remains an ESS. This turns out to be true whether the costs of aggression are the same for all players, or instead individually variable. If the latter is true, the expected outcome is for animals that can best sustain the costs of aggression to sport large badges and be most aggressive; those with less resilience to these costs will have small badges and be subordinate. They note that the badges would then constitute honest indicators of physical condition, and be useful for functions above and beyond social status. For example, females might use badge size as an indicator of suitor health even though the original function of the badges was to signal aggressive status. There is evidence in several bird species that badges both determine male status and attract female mates (Møller 1988a; Norris 1990a,b).

Johnstone and Norris thus argue that two different costs must exist to ensure honest badges of status: a risk that cheats will be challenged and suffer the full costs of fights, and a general cost of being aggressive that is independent of badge size or escalation rates. What might impose the latter costs? They and other authors note that testosterone is frequently a mechanism for modulating aggression in vertebrate animals. Testosterone levels are also known to impact immune systems adversely (Alexander and Stimson 1988; Folstad and Karter 1992; Grossman 1985; Wedekind 1992; Zuk 1990). The high testosterone required to be aggressive may thus impose a cost on the animal's immune system. High testosterone levels may also reduce survivorship by increasing metabolic or time costs or by increasing predation risks (Hogstad 1987; Røskaft et al. 1986). This appears to be the case in at least one lizard species (Marler and Moore 1988, 1989).

Badges clearly play a role in settling priority of access to resources or mates in some species; not surprisingly given the models, they appear to be honored only when benefit to cost ratios or the chances of subordinates winning a contest are low (Evans 1991; Evans and Hatchwell 1991; Fugle et al. 1984; Hansen and Rohwer 1986; Jarvi and Bakken 1984; Marchetti 1993; Møller 1987a,b, 1988a; Norris 1990a; Parsons and Baptista 1980; Petrie 1988; Rohwer 1977, 1985; Rohwer and Ewald 1981; Røskaft and Rohwer 1987; Searcy 1979; Studd and Robertson 1985; Whitfield 1987). In house sparrows, both types of costs required by the Johnstone and Norris (1993) models have been described. The bearers of deceitfully large badges are severely punished by other large-badged birds (Møller 1987b), and large-badged birds bear a contest-independent cost of increased autumn mortality (Møller 1989). Not all studies have shown the presence of both kinds of costs. In fact, in several other species of sparrows, experimental enlargement of badge size allowed cheats to prosper without serious punishment (Fugle and Rothstein 1987; Rohwer and Rowher 1978). In at least one case, the badges seemed not to be in-

dicators of status but instead related to differential foraging roles within the group (Rohwer and Ewald 1981).

Honesty and Begging

In mate choice and agonistic situations, a receiver seeks information to identify which of several responses will best benefit itself. The fact that the receiver's choice may benefit the sender is often incidental to the receiver's interest in the interaction. Begging is somewhat different. Here the sender tries to persuade the receiver to perform an action whose sole purpose is to benefit the sender at a direct cost to the receiver. Presumably, receivers would not perform this action unless there were some compensatory deferred or indirect benefits. For example, the sender and receiver might be genetic relatives (kin selection). Alternatively, perhaps helping the sender now will ensure help to the receiver should the roles be reversed at a later time (reciprocity). An honest sender would only beg when it truly was in need, and it would adjust its level of begging to match its need. But why should a beggar be honest? What can receivers do to prevent being deceived about sender needs?

This situation has been modeled by Maynard Smith (1991, 1994) as the Sir Philip Sidney game. The name refers to a story about a wounded British officer who had to choose between donating his last water to a begging wounded soldier or keeping it for himself. Maynard Smith's version of the game was a 3×3 discrete asymmetric contest. The possible sender strategies were: (a) only beg when in need, (b) always beg regardless of need, and (c) never beg. Receiver strategies were: (a) only give to senders when they beg, (b) always give to senders regardless of their actions, and (c) never give to senders even if they beg. As always, the solution of this game depends on the relative values of benefits and costs accruing to each party given each combination of strategies played. Maynard Smith assumed that the two parties were at least partially related genetically, and thus allowed for a kin selection repayment to the donor. When critical parameters are favorable for communication despite a conflict of interest, there are two ESSs: (a) the sender never begs and the receiver ignores all signals, and (b) the sender only begs when in need, and the receiver only gives when the sender begs. The latter ESS, which is basically honest signaling, turns out to be possible only if begging imposes some nonzero cost on senders. This cost could be a loss of energy or time during begging (necessary costs), a risk of later punishment if found cheating (incidental costs), or both. We thus find again that honest signaling requires imposition of some handicap cost on the sender. One other outcome of Maynard Smith's analysis is that if sender and receiver do not have a conflict of interest, honest signaling can then evolve without the requisite handicap costs; note that only a similar ranking of alternative outcomes, and not a quantitative identity of interests, is required in this case.

The Sir Philip Sidney game has also been modeled by Godfray (1991) and by Johnstone and Grafen (1992a) with both sender need and sender begging level as continuous variables (a continuous asymmetric contest). In the latter study, the two parties are relatives, but the coefficient of genetic relat-

edness between them is allowed to vary continuously. Not surprisingly, receivers never give unless the sender is sufficiently closely related. Thus it does not pay the sender to beg much from distant relatives. By the same token, receivers give readily to very close relatives; the latter need not beg much to elicit the response. As a result, the ESS is for senders to adjust begging effort, and thus costs, as a function of genetic relatedness to the receiver; maximal costs will be expended by a sender begging from relatives of intermediate relatedness. And it is again these costs that guarantee honesty.

Begging, broadly defined, occurs in many animal species. Perhaps the best studied system is begging by altricial nestling birds (Figure 20.7). It is widely recognized that parents and nestlings are likely to differ in the amount of investment a parent should make in any given offspring (Bengtsson and Ryden 1983; Godfray 1991, 1995b; Gottlander 1987; Harper 1986; Henderson 1975; Hussell 1988; McGillvray and Levenson 1986; Mondloch 1995; Redondo and Castro 1992a; Stamps et al. 1989; Trivers 1974). For nests with a single offspring, the parents must optimally allocate their efforts and risks between this current individual and any future ones; the current nestling will usually want more care than is optimal for the parents to give and may thus be tempted to beg dishonestly. When nests contain multiple offspring, parents must choose between equal allocations to all nestlings, or favored investments in selected individuals. Should nestlings beg according to need or should even those without need beg vigorously? The single nestling case has been modeled by Godfray (1991). An ESS for honest begging by a nestling is assured only if begging is costly, and the benefits of the begging are higher for those truly in need. Note the difference from other functional categories where senders differ in the costs but not in the benefits of signaling. Sender costs are still required for an ESS. What might they be? In addition to the energy expended during vigorous begging, several authors have pointed out that begging makes nestlings more conspicuous to nest predators (Haskell 1994; Redondo and Castro 1992b). We discuss these models further in Chapter 24.

Begging occurs in many other contexts but has received less theoretical attention. Juvenile primates use special expressions and sounds to solicit food tidbits from adults, and adult chimpanzees will beg from other adults that have just killed a monkey (Boesch and Boesch 1983, 1989). Female magpie jays beg food from visiting males to avoid having to leave the nest (Langen 1996a). Adult vampire bats that have failed to feed return to their day roost at dawn and use specific behaviors to beg for regurgitated blood from roostmates (Wilkinson 1984). Social insects such as bees, ants, wasps, and termites beg for food collected by returning foragers (Michelsen et al. 1986; Wilson 1971). Individuals in at least the insect colonies are highly related genetically; the Johnstone and Grafen model would predict that begging among the insects would require only minor sender costs to guarantee honesty. Distress calls in which a frightened or threatened animal signals for assistance also may be considered begging (but see discussion on pages 846–847). In few of these examples have both the costs of signaling and the degree of honesty been assessed.

Figure 20.7 Begging signals by altricial nestling birds. Typical nestlings wag their heads, show brightly patterned and gaping mouths, and emit sounds as they beg for food from parents. Game-theoretical models suggest that nestling begging will only be honest if signal production is costly and the benefits of begging are higher for those that most need feeding (Godfray 1991, 1995b). Although there seems to be little energetic cost to nestling begging (McCarty 1996), increased attraction of predators when nestlings beg may provide sufficient incentive to insure signal honesty (Haskell 1994; Redondo and Castro 1992b). (Photo courtesy of Marc Dantzker.)

Honesty, Amplifiers, and Attenuators

Amplifiers are a special case of a handicap whose very function penalizes those individuals most tempted to cheat. The aim of such traits is to make it easier for direct assessment of sender qualities by a receiver. Clearly, animals of low quality would do better to hinder such assessment, not promote it. Exhibiting an amplifier thus has a higher cost (and probably less advantage) to a lower-quality animal than to a higher-quality one. Attenuators are the opposite type of signal; they make direct assessment of some trait by a receiver more difficult.

Can amplifiers evolve despite the costs to low-quality individuals? Amplifier evolution has only been examined with genetic models, but the results are similar to those one would obtain using game theory (Hasson 1989, 1990; Hasson et al. 1992). Regardless of genetic assumptions, amplifiers can evolve as long as high-quality individuals are sufficiently common, the benefits to high-quality individuals of displaying an amplifier exceed the costs, and low- and high-quality individuals differ sufficiently in fitness that average fitness benefits of the trait to high-quality individuals are greater than the average costs to fitness suffered by low-quality ones. Note that if low-quality individuals respond to the costs by failing to exhibit the amplifier, the simple presence or absence of the amplifier trait becomes an honest indicator of sender quality (e.g., the amplifier evolves into a signal). Note also that the evolution of amplifiers does not require an additional cost to guarantee honesty; honesty is the whole point of amplifier function.

Attenuators can evolve in a population if low-quality individuals are sufficiently common relative to high-quality ones (Hasson et al. 1992). However, the dynamics are different from those of amplifiers. Amplifier expression leads

selectively to higher fitnesses for high-quality individuals. The latter become relatively more abundant over time, and this eventually favors amplifiers over attenuators. Attenuators, if successful, result in random receiver choice and thus do not selectively favor low-quality individuals in particular. This makes the evolution of attenuators slower and less stable than amplifiers.

Honesty and Predator Notification

A final type of signal we shall consider here is that sent by prey to dissuade predators from chasing them. There are two classes of such signals (see detailed treatment in Chapter 25). First, the prey may perform some display of agility, speed, or stamina that indicates its ability to escape if chased. One example is stotting by gazelles to a nearby cheetah or wild dog (Fitzgibbon and Fanshawe 1988). The second class of predator signal is some action (e.g., a snort, whistle, or tail flash) that all prey perform the same way to let the predator know it has been spotted and therefore attack is unlikely to be successful. Both kinds of predator signal can evolve into honest indicators of relative prey vulnerability. How well the first class of signals is performed can be an honest measure of prey condition. The proximity that prey allow a predator to achieve before giving the second class of signal can be an honest measure of the prey's confidence that it would escape any attack. Vega-Redondo and Hasson (1993) have shown that honest indications of vulnerability are only evolutionarily stable if there is a cost to the sender that is greatest for low-condition animals. The energetic costs and the drawing of predator attention would seem to meet these conditions for the first class of signal. Being too close to a predator before giving a signal of the second class would also constitute such a cost. As with most other cases we have examined, differential costs appear to be a necessary condition for honest signaling of prey vulnerability.

ERRORS, SIGNAL EVOLUTION, AND HONESTY

The prior models all imply that deceit will be rare or absent in animals. Yet, we know that this is not the case. Mantis shrimp that have recently moulted and are thus vulnerable in an escalated fight will bluff and produce threat displays as if there were no problem (Figure 20.8; Adams and Caldwell 1990; Steger and Caldwell 1983). Foraging birds will falsely emit alarm calls to scare competitors away from food finds (Møller 1988b). A number of primates are known to practice quite complicated patterns of deceit (Byrne and Whiten 1988; de Waal 1986). Although deceit is less common than honesty, it does seem widespread in nature. In fact, mixtures of honesty and deceit may be the rule (Bond 1989; Dawkins 1993; Gardner and Morris 1989). There are at least three explanations for why some deceit may be present even when most signals are honest: (a) perceptual error by receivers allows some cheaters to escape detection, (b) evolving signaling systems have yet to reach the ESS, and (c) a single type of receiver may have to deal with multiple senders. We take up each of these in turn below.

Table 20.2. Summary of evolutionary models of honest signaling

Function	Sender strategies	Game type	Honesty conditions	References
Agonistic contests	Select display according to effectiveness and cost to sender. Honest sender selects display indicating true motivation; selection of dishonest sender exaggerates true motivation.	Discrete asymmetric contest	Requires a positive correlation between display effectiveness and sender cost.	Enquist 1985; Enquist et al. 1985
Courtship	Display with intensity higher than competitors, to attract mates. Honest senders adjust intensity to match relative quality assayed by females; dishonest senders exaggerate by giving higher intensity than justified by quality.	Continuous asymmetric scramble	Display must be costly to senders, with greater costs at given intensity for lower-quality males.	Grafen 1990a,b
Badges of status	Display badge with size indicating dominance rank. Honest senders adjust badge size to reflect true status; dishonest senders sport badge with either too large or too small a size.	Continuous symmetric contest	Cost of escalated fights must increase with badge size, and large-badged animals must be challenged often by other large-badged animals.	Maynard Smith and Harper 1988
		Discrete symmetric contest	Same as above plus there must be a contest-independent cost of being aggressive.	Owens and Hartley 1991; Johnstone and Norris 1993
Begging (Sir Philip Sidney game)	Sender signals demand for help to receiver. Honest senders only signal when in need; dishonest senders always signal. Receiver benefits only indirectly from giving to sender.	Discrete asymmetric contest	Begging must be costly to senders.	Maynard Smith 1991
		Continuous asymmetric contest	Sender costs are highest when an intermediate level of relatedness between sender and receiver exists.	Godfray 1991; Johnstone and Grafen 1992
Amplifiers	Display trait facilitating accurate direct assessment of sender qualities. Honest sender sports amplifier; dishonest sender shows attenuator.	Genetic models	Amplifiers can evolve if average benefits to high-quality senders are greater than average costs to low-quality ones.	Hasson 1989b, 1990; Hasson et al. 1992; Michod and Hasson 1990
Predator notification	Prey display to predator that they are not worth chasing. Honest sender shows true agility or condition; dishonest sender uses noninformative display.	Continuous asymmetric contest	Display must be costly, with lower-quality senders paying higher cost for a given display level.	Vega-Redondo and Hasson 1993
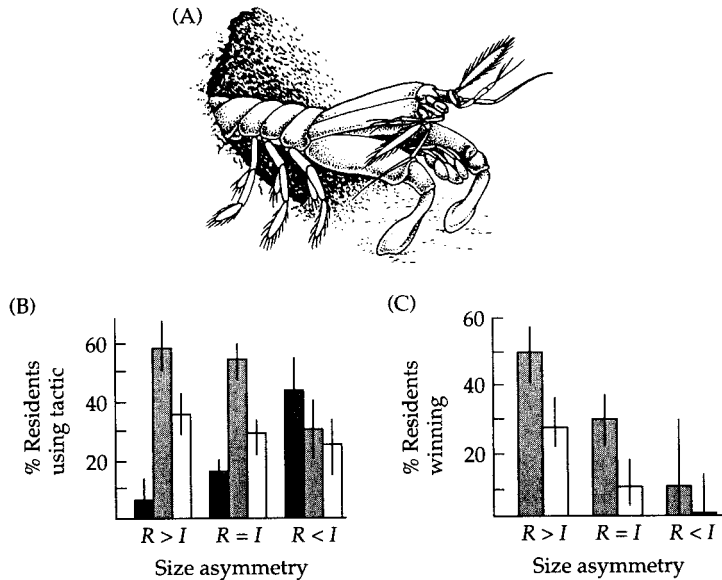
Figure 20.8   Bluff in the threat display of resident mantis shrimp (*Gonodactylus bredini*). Tropical mantis shrimp live solitarily in burrows in coral reefs. Suitable holes are in short supply, and fights between residents and intruders are vigorous and even lethal. (A) One of several displays used by a resident to threaten approaching intruders that are not too much larger than the resident. When intruders are not larger, threat display is sufficient to ward off attack in more than half of intrusions. Residents often flee without display if intruders are sufficiently larger. Adult mantis shrimp moult every two months. For three days postmolt, their exoskeletons are soft and they are easily injured or killed in an escalated fight. At most, 20% of animals on a reef are in this vulnerable condition. Despite their soft exoskeletons, many recently moulted residents bluff by giving the threat display even though they will be unable to back it up with attack. (B) Fractions of newly moulted residents that flee (dark bars), threaten (hatched bars), or do nothing (open bars) as intruders of different relative sizes approach. *R* and *I* refer to relative sizes of resident and intruder respectively. Threats are more common than fleeing or inaction when intruders are no larger than residents, but flight becomes the dominant response when intruders are larger ($G = 39.89; df = 4; p < 0.001$). (C) Fractions of intrusions won by newly moulted resident if it threatens the intruder (hatched bars) versus does nothing (open bars) for different relative sizes of intruder. Chances of retaining residence are significantly enhanced ($p < 0.05$ or smaller) if newly moulted resident threatens intruders of similar or smaller size. Thus these animals show a low but persistent level of dishonest signaling that is significantly effective to the detriment of receivers (Adams and Caldwell 1990; Steger and Caldwell 1983). (A after Trivers 1985; B, C after Adams and Caldwell, 1990.)

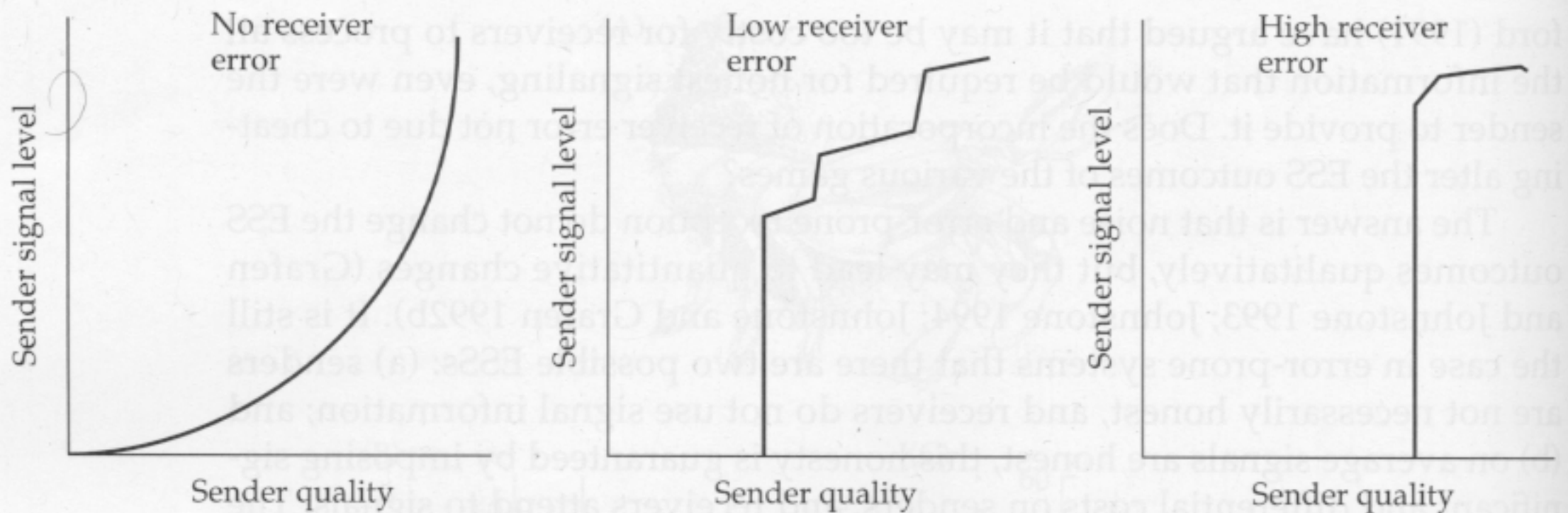## Signaling Games When Receivers Have Perceptual Errors

All of the models in the prior section ignore receiver error due to causes other than dishonesty. However, we saw in Part II that few signaling systems will favor (for economic reasons) or allow (for physical ones) the provision of perfect information and that some receiver error is the rule. Dawkins and Guil-

ford (1991) have argued that it may be too costly for receivers to process all the information that would be required for honest signaling, even were the sender to provide it. Does the incorporation of receiver error not due to cheating alter the ESS outcomes of the various games?

The answer is that noise and error-prone reception do not change the ESS outcomes qualitatively, but they may lead to quantitative changes (Grafen and Johnstone 1993; Johnstone 1994; Johnstone and Grafen 1992b). It is still the case in error-prone systems that there are two possible ESSs: (a) senders are not necessarily honest, and receivers do not use signal information; and (b) on average signals are honest, this honesty is guaranteed by imposing significant and differential costs on senders, and receivers attend to signals. The term "on average" acknowledges the fact that not every signal emitted is going to be correctly interpreted by a receiver; however, reliable information must be provided often enough to justify receiver attention. These results allow generally honest signaling to be compatible with simple optimality constraints on the sending and processing of information and thus resolve the problem raised by Dawkins and Guilford. On the other hand, they raise the question of what determines the relative roles that honesty guarantees and optimality constraints play in different signals; surely the ratio varies, and how it is related to function and context is critical to understanding signal diversity (Dawkins 1993).

Quantitative effects of adding error to the ESS analyses are interesting. One common property of complex games is that each combination of possible strategies must be likely to occur or else it may be impossible to move evolutionarily from certain initial states to the ESS. In game theory parlance, all relevant strategies must be tested at least occasionally. Adding player error to such games resolves this problem because now, by chance, all possible combinations of roles and strategies are possible, and nearly any evolutionary trajectory is likely to occur sometime. This same principle applies to signaling games. Adding receiver error makes the predicted ESSs more likely and thus more globally stable.

· The second change of adding receiver error is that it may no longer be optimal for senders to display with exact honesty. If two males differ in quality by 10%, and receiver error is at least that high, why should the higher-quality male advertise 10% more energetically than its competitor? The female is likely to perceive them as the same and thus the extra output by the higher quality male will be wasted. In error-free situations, the signaling ESS is a smooth monotonic function relating display investment to sender quality (Figure 20.3). The corresponding ESS functions when there is perceptual error are step-shaped; the more receivers err, the fewer the number of steps and the wider each step (Figure 20.9). Since a given animal is just as likely to be confused with its next higher ranking competitor as with its next lower one, where the steps occur is arbitrary, and there are thus many alternative ESS functions. When error is very high, the ESS is for most low-quality males to display at one low level or not at all, and higher-quality ones to display at another higher level (Grafen and Johnstone 1993; Johnstone 1994).

Figure 20.9   **Effect of receiver error on ESS sender strategies for handicap models of signaling.** When receivers have no perceptual error, the ESS is for senders to adjust the display level according to a monotonic function relating sender quality to display (left). When there is even some receiver error, low-quality senders should produce no display or a minimal one; higher-quality senders should display according to a stepwise function in which there is rough matching of quality rank and signal rank, but within clusters of similar senders, all should display at the same level (middle). For high receiver error, senders are effectively divided into two groups: low-quality individuals, who do not display, and high-quality ones, all of which display at nearly the same level. (After Johnstone 1994.)

This model thus provides an alternative explanation for the widespread use of stereotyped all-or-nothing signals given at typical intensities (as described on page 519). Stereotypy is simply the honest ESS when receiver perceptual error is high. This contrasts with simple optimality arguments that stereotypy evolves to ensure accurate signal transmission and detection. A third explanation is that posed by Zahavi (1980, 1987, 1993) and discussed on pages 652–653. He argues that receivers force senders to perform displays according to some standard. A good match to the standard indicates a high value of the quality receivers seek to measure. It is not easy to come up with tests that discriminate conclusively among these alternatives. Certainly, none of the explanations are incompatible with the others, and all may play some role in real systems.

Evolutionary Equilibria versus Systems in Continuous Flux

Is it reasonable to treat all signal systems as if they were at an evolutionary equilibrium? Is there any stage in the evolution of new signals when senders have the upper hand and cheating is common (Dawkins and Krebs 1978)? Andersson (1980) argued that animals have many more threat displays than they appear to need because many signals are the now uninformative relics of prior arms races between senders and receivers; new signals that recapture the attention of receivers would always be favored.

We discussed the mechanisms by which new signals might evolve in Chapter 16. Not all of these would seem to favor honest signaling at least at the outset. We take up the special case of Fisherian sexual selection in Chapter

23. Sensory exploitation of receivers was reviewed on pages 526–534. Here, senders produce signals that trigger latent receiver preferences to the detriment of the receivers (Basolo 1990; Leimar et al. 1986; Ryan 1990; Ryan et al. 1990; Staddon 1975). Such signals are initially dishonest. Can we expect them to evolve to honest ESSs or is such dishonesty stable?

Krakauer and Johnstone (1995) have examined a neural net simulation in which there are two players: a sender and a receiver. The model population was similar to that studied by Enquist and Arak (1993) and outlined in Box 16.2, but here allowed both senders and receivers to evolve. Senders varied in some quality that receivers wished to assess accurately. They produced multidimensional signals that were the only source of information to receivers. Each party used a three-layer neural net to deal with signal exchanges. The sender's net generated signals indicating its quality (honestly or falsely) and the receiver's net evaluated the signals to find the sender with the highest quality. Receivers locating the highest quality senders had the highest "fitness" and were thus made more common in the next generation. Sender representation in the next generation depended on the number of times each was chosen by a receiver and any costs they had to pay for signaling. Each generation, mutations occurred that varied the linkages in the neural nets allowing for new sender and receiver strategies. This world was allowed to coevolve until strategies stabilized or until some maximum number of generations had passed. The model thus examined the coevolution of sender and receiver using simple neural processing. Two different worlds were considered: one in which senders could produce signals without any costs to themselves, and one in which signals were differentially costly as a function of sender quality and thus potential handicaps.

The results of these simulations are illuminating. When signaling is cost-free, mean fitness of senders tends to increase steadily with successive generations, whereas receiver fitnesses remain low at levels similar to that when no information is being provided. The increase in sender fitness arises largely from sensory exploitation of latent receiver preferences. When signaling is differentially costly, sender fitness remains near its initial levels, but receiver fitness rises and plateaus at a higher value. The more signal dimensions that are used by the receiver, the higher this eventual receiver fitness. Thus, if costly signaling is allowed, signals are on average honest both in the final equilibrium and during much of the history. However, the simulations with signal costs clearly show periods in which mutant senders hit on signals exploiting latent biases of receivers. For a period, sender fitness increases and receiver fitness drops. But this is invariably followed by the appearance of mutant receivers that devalue the exploited biases and focus on other more honest signal dimensions. Receiver fitness then rebounds and sender fitness drops back to lower levels. These episodes recur over time because each change in sender signals causes a change in optimal neural net linkages in the receiver. This invariably generates new latent biases in receivers that future sender mutants can exploit. The process is thus inherently never-ending. This coevolutionary dynamic is exactly the kind of process envisioned by Dawkins and Krebs

(1978) and Andersson (1980). However, it is also compatible with the handicap principle because costly signals are honest at least on average and over long time scales.

Multiple Senders and Single Receivers

All of the game models on pages 654–668 assume a single class of senders, and so the ESS is a single rule for mapping information onto signal form or frequency. What if there are several classes of senders with different stakes and potential costs? This situation has been examined by Johnstone and Grafen (1993) using the Sir Philip Sidney game as an example. They allow there to be two classes of begging senders: one that begs honestly, and one that always begs regardless of need. The latter are thus cheats some of the time. Receivers cannot tell the two types apart. The ESS is for receivers to respond to all begging as long as honest beggars are more closely related to receivers, and/or honest beggars pay a higher cost for begging than do constant beggars. It must also be the case that honest beggars are sufficiently common relative to constant beggars. How common they must be depends upon the cost to receivers of responding to a constant beggar that is cheating. The higher this cost, the higher the fraction of honest beggars required to justify receiver response.

Johnstone and Grafen argue that variation in sender economics is likely to be common and so should be the existence of multiple sender classes. What is critical to this ESS mixture of honesty and deceit is that receivers cannot discriminate between the multiple classes of senders. Were they able to, then they would use different interpretive rules for signals from each class and honesty would be assured. This may be what is occuring in mantis shrimp where vulnerable and invulnerable senders cannot be distinguished without a risky close approach, but vulnerable senders are clearly a minority of the population (Figure 20.8). In a way, deceit is here seen again as a consequence of imperfect receiver assessment. However, it is precisely because receivers cannot assess everything directly that they have recourse to signals in the first place. Thus it may not be surprising that they are sometimes also unable to assess different sender classes. If all of this is so, it provides a very widespread reason for why most signaling systems should be largely honest, but exhibit some persistent low levels of deceit.

SUMMARY

1. **Deceit** is the provision of inaccurate information by a sender to a receiver. It is associated with a positive value of information for the sender, but a negative value for the receiver. Types of deceit include **lies** (use of the wrong categorical signal when alternatives are few and discrete), **withholding information** (not giving a signal when appropriate), **exaggeration** or **bluff** (using a signal whose rank among ordered alternatives is different from that for the corresponding condition values), and **attenuators** (traits that make it more difficult for a receiver to directly assess some trait). The opposite of deceit is **honest signaling**.

2. Early ethologists focused on the evolutionary sources of signals. They presumed that most signals were honest because they were obligately linked to the motivations prompting them. Behavioral ecologists focused on the strategic importance of signals, and many concluded that animal communication was an arms race between deceitful senders and sceptical receivers and thus rarely honest. Zahavi proposed the **handicap principle** that says that receivers should only attend to signals sufficiently costly to senders that it does not pay to cheat. Put another way, signals should impose **handicaps** on senders to ensure honesty.

3. The outcomes of game-theoretical treatments of honest signaling might be expected to differ depending upon the nature of the information provided during communication, the degree to which a receiver can compare signal information to direct assessment or prior expectations, and the nature of the costs of sending signals.

4. Nearly all models of honest signaling between parties without similar interests conclude that honesty can be guaranteed only if receivers demand signals that impose a higher cost on deceitful than on honest senders. **Agonistic signals** can be honest indicators of sender motivation as long as the more costly signals are the more effective ones. Females choosing mates should favor **courtship signals** that are costly to displaying males, and costly in a way that tests mate suitability. **Badges of status** will be honest only if large badges are challenged by other large-badge individuals, and there is a contest-independent cost of being aggressive and seeking high rank. **Amplifiers** are inherently more costly to potential cheaters than to those that most benefit from honesty. **Begging** and **predator notification** signals are both unlikely to be honest unless they impose costs on senders that are higher for potential deceivers. In most of these models, differential handicap costs lead to honest signals, and honest signals are possible only if there exist differential handicap costs. Many studies of animal communication support the notion that signals are usually honest and costly to senders.

5. Although the simple game models predict that animal signals will always be honest, most animal communication systems exhibit a mixture of honesty and deceit, with deceit being the more rare moiety. This outcome is in fact predicted by modified game models in which receivers are allowed to err in their identification or interpretation of signals, communication systems are allowed to continue evolving over time, and it is recognized that any given receiver may encounter multiple classes of senders each with its own costs and benefits of signaling. Part II of this book argues that all of these are likely conditions in nature.

FURTHER READING

Concise and very readable introductions to these issues can be found in Harper (1991) and Johnstone (1997). Wiley (1994) reviews the interface between deceit on the one hand, and other sources of receiver error on the other. Hasson (1994) pro-

vides a useful classification of the different ways in which senders may deceive receivers. Zahavi's own presentations (1980, 1987, 1993, Zahavi and Zahavi 1997) of the handicap principle are full of ideas and examples that will stimulate a reader's thinking about these issues. Grafen's (1990a,b) pivotal papers on signal honesty are difficult but entertaining reading. Advanced readers are encouraged to work through them, as Grafen is very good at identifying the critical steps and consequences of his models. Dawkins (1993), Dawkins and Guilford (1991), and Guilford and Dawkins (1995) provide important perspectives on the interface between simple optimality (Part II) and game-theoretical (Part III) approaches to animal communication. This interface is bound to be a major focus of future research. Finally, neural net simulations have provided many new insights into signal evolution. Studies by Arak and Enquist (1993), Enquist and Arak (1993, 1994), and Krakauer and Johnstone (1995) are surely only the beginning of this approach.

Principles
of Animal
Communication

Jack W. Bradbury
Sandra L. Vehrencamp

Department of Biology
University of California, San Diego