



Towards a General Theory of Biological Signaling

OREN HASSON

*Department of Entomology, Faculty of Agriculture, The Hebrew University of Jerusalem, P.O.
Box 12, Rehovot 76100, Israel*

(Received on January 1996, Accepted on May 1996)

Current models of biological communication point at evolutionary mechanisms of particular signal types. Those that present complete models look at the signals' equilibrium values and their evolutionary stability, and require two simultaneous equations: an equation that describes the signaler's fitness as a function of the signal and of the recipients' response, and a simultaneous equation that represents the fitness of recipients. This paper examines the effect of different signal types, such as handicaps, amplifiers, camouflage, mimicry etc, on the first equation. By considering parameters that affect the evolution of signals this paper first constructs a general model of biological signaling. Different signal types are then characterized by different sets of limiting assumptions. As a result, the fitness of a signaler of each signal type is represented by a unique equation that is a mathematical derivation of the general signaling model. This analysis enables a natural division of signals into groups and subgroups that share similar assumptions and properties. It shows the importance of signal design, and points at three methods by which signals may be reliable: by trade-offs between cost and benefits, by design and by convention.

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1. Introduction

Communication is so widespread in the biological world, that we probably can use it to characterize life. Yet, despite the number of theories that explain the evolution of specific signal types, and the immense amount of data on their effects on signalers and recipients, there has been no serious attempt to provide a general and comprehensive theory of communication. The few attempts to construct models of communication that may be applied to different types of communicators were mostly concerned each with a single signal type (Nur & Hasson, 1984; Zahavi, 1987, 1991; Grafen, 1990; Maynard Smith, 1991a, b; Hasson *et al.*, 1992).

Here, I formalize a definition of signals that embraces both cheating and reliable signals (Hasson, 1994), to construct a general signaling model, aimed to show the necessary and sufficient parameters that affect signal evolution. I then characterize different signal types by different sets of restricting assumptions, and hence by different equations that are mathemati-

cal derivations of this general equation. Putting assumptions and definitions that underline the evolution of different signals into a concise, simple and general model enables a more precise and complete view of signaling than is found in previous attempts. Moreover, this model allows me to re-evaluate previous suggestions regarding the role of signal design (Zahavi, 1978; Dawkins & Guilford, 1991; Hasson, 1991a, b) and to explicitly show its importance in the evolution of signals. Finally, this model points at three different ways by which signals may be made reliable.

2. A General Signaling Model

2.1 SIGNAL SELECTION

Most characters evolve as a result of trade-offs between particular costs and benefits. Signals are no exception. However, signals are different from all other characters in that their benefits are bestowed by other individuals, termed the signals' recipients

(Hasson, 1994). Where “signalers” and “recipients” are cells within a same body, or where an individual may receive its own “signal” later in time (such as bees’ scent-marks on flower; Giura & Nunez, 1992; Schmidt & Birch, 1990), there is no conflict of interest between signaler and recipient, though transferred information might need to be checked for errors. Such “signals” may work by the same principles as those described here, though the evolutionary forces that make them work are different. This paper only discusses cases in which the signaler and recipient are not the same evolutionary entity.

Let F denote the signaler’s basal fitness component, and S the (social) component that changes as a result of the recipients’ response to the signal (Hasson, 1994). Any investment in signal, denoted as x , changes its expression while imposing costs on F . Hence, x may change a signaler’s characteristic such as tail length, song duration, color intensity, etc, or result in a shift in the function or in the frequency of use of an already existing characteristic or behavior. For convenience of discussion, I hereafter refer to x as its perceivable approximation, signal intensity. Any increase in x causes costs in F . Therefore, in order to evolve $S(x)$ must be positive, at least on average (and, often, sufficiently high to overcompensate for costs in F). Fitness of a signaler is therefore given by an equation that should have the general form:

$$W = G\{F[Q(x)], S[x]\}, \quad (1)$$

where, on average, $dF/dx < 0$ and $dS/dx > 0$; Q represents the signaler’s “quality”. Its division into three separate components is shown below to be crucial to the understanding of signals. Equation (1) simply states that the fitness of a signaler can be regarded as the interaction (G) between the two fitness components, where F is negatively correlated with the signaler’s investment in the signal, and S is positively correlated with it.*

We can use the notations we have just developed to define signals as traits that impose a non-negative cost on their bearers’ F -component, and a positive specific effect on their bearers’ S -component stemming from their potential to influence the behavior of other individuals. The influence on other individuals’ behavior usually occurs through changing their “information state”, used here in its biological sense to indicate the choice of the recipient’s subsequent

strategies (Hasson, 1994). If, on the average, the resultant choice of actions improves the recipient’s fitness, we recognize that a signal is reliable; if it decreases its fitness, we recognize that a signal is cheating (Hasson, 1994).

Equation (1) depicts the actions of natural selection and signal selection (Zahavi, 1987, 1991). Natural selection describes the state in which selection on x is determined by interactions in F alone, i.e. where $dS/dx = 0$. Consequently, if \hat{x} denotes the x value that maximizes fitness then, in response to natural selection only, fitness is maximized at $\hat{x} = x_0$ (where $dF/dx = 0$, i.e. where F is maximized by natural selection acting alone). Signal selection is described by $dS/dx > 0$, and usually leads to fitness maximization at $x = \hat{x}$, defined as x_0 , where $dF/dx < 0$. Darwin (1871) contrasted natural selection and sexual selection, and Zahavi’s generalization that contrasts natural selection with signal selection (Zahavi, 1987, 1991) seems to be at least as useful as Darwin’s. However, “signal selection” critically depends on how signals are defined. Since the definition of signals here is much more inclusive than in Zahavi (1987, 1991), it follows that the definition of signal selection is also more inclusive.

The distinction between signal selection and natural selection is now useful for making a clearer distinction between “signals” and “cues”, both of which have an effect on recipients’ information state. Signals evolve by signal selection because they change recipients’ information state, despite their negative effect on the signalers’ F . Cues, in contrast, such as prey age or size, may be non-heritable or evolve by natural selection alone. They confer no costs on F and are sometimes maintained despite the fact that they change recipients’ information state. This distinction may be formalized as follows:

Signals are characterized by $dF/dx < 0$, $dS/dx > 0$, and $\hat{x} > x_0$. The first expression describes costs conferred by the signal, the second, signal selection, and $|\hat{x} - x_0| > 0$ gives the signal expression (signal selection can potentially lead also to $\hat{x} < x_0$, such as short tails rather than long ones; for simplicity of further discussion I hereafter address only the $\hat{x} > x_0$ case). Cues are described by $dS/dx \neq 0$, $\hat{x} \approx x_0$, and $d\hat{x}/dQ > 0$. The first expression describes the recipients’ response, whose effect on the cue’s carrier may be positive or negative, the second, no special evolution as a result of this response, and the third, the cue’s informative nature at the equilibrium point. Although recipients respond to cues, the cues’ further development must be inhibited, or they become signals. At equilibrium, this may be either because a cue’s further development is strongly constrained, or

that the mathematical operation that I use here, either simple or partial derivatives (e.g. dF/dx , or $\partial F/\partial Q$, respectively) are only used as the shorthand to indicate the type of change (slope) of one variable with respect to another (hence, F decreases with x , but increases with Q).

because variations in its expression are purely phenotypic (Hasson, 1991a). Cheating signals only differ from reliable signals by their effect on the recipients' fitness, not by any other requirement described above (Hasson, 1994).

The theory of communication thus focuses on three elements: (a) the forces that initiate signal evolution (leading to $x > x_0$), (b) the signal expression at equilibrium and the mechanisms that lead to its determination, and (c) the stability of this equilibrium. Here I focus on the first element, touching very briefly on the second and third elements. Elements (b) and (c) that deal with equilibrium points and their stability can be determined by full communication models that include two simultaneous equations: one that describes the signaler's fitness, and another that describes the recipient's fitness as a function of the change in its information state in response to the signal. This must be done separately for each signal type (e.g. see Grafen, 1990; Maynard Smith, 1985, 1991a; and references therein), and is beyond the scope of this paper. Instead, the goal of this paper is to develop a general model of signaling by extending the first equation to its most general form, use it to explore the possible forces that lead to signals' evolution, formally classify signals into different types, and show some possible (evolutionary) interactions and (logical) relatedness among them.

Organisms use information to evaluate expected costs and benefits of their future actions. For constructing this model I divide information into three distinct categories that lead to different evolutionary mechanisms, hence to different sets of signals. These are the signaler's quality, its needs, and external factors not related to the signaler but which may nevertheless affect the recipient and, *via* its reaction, also the signaler's S . Maynard Smith & Harper (1995) call the first two "self report", and the latter, "other report". At least most information regarding two other important variables, the signaler's motivations and intentions, can probably be revealed (or concealed) by using signals that change information about quality, needs, or even external factors, because they are affected by them. Hence, signals that give information about quality, needs and external factors can probably be used also to make inferences about motivations and intentions (see also the Discussion).

2.2. EXTERNAL FACTORS

Equation (1) represents the signaler's fitness in only a simplistic form. To make it more general we need to introduce two additional variables. One

denotes external factors, unrelated to the signaler's quality, which may nevertheless affect the recipient, and the other is a dichotomous variable that describes the "environment" in which a signal interacts with recipients. In addition, we need to deal more properly with the signaler's quality and needs. These tasks are achieved in this section and in the two sections that follow.

Information about facts or events that are not directly related to the signaler's quality (such as approaching predators) may change the behavior of other individuals in a way that affects the signaler's fitness. Charnov & Krebs (1975), for example, hypothesize that a bird in a flock may give a warning signal on a predator's approach to position itself behind its fleeing flock mates. Here, the change in behavior of the signaler's flock mates, as a result of their novel information about the approaching predator, mainly benefits the signaler (no information is given about the predator's location!). Recipients can make correct or incorrect inferences about these facts or events by inspecting other individuals, considering both cues (such as alertness behavior) and signals (e.g. alarm calls). By denoting the state of the external facts and events with E (specifically those, such as predation risk, which may affect the recipient's choice of strategies that, in turn, influence the signaler's S), we get:

$$W = G\{F[Q(x)], S[E, x]\}. \quad (2)$$

2.3. THE SIGNALER'S QUALITY

A proper treatment of quality requires two independent steps. The first is achieved by noticing that recipients may assess the signalers' quality by examining cues only, signals only, or a combined effect of both signals and cues. For example, a female bird may assess males by examining their overall conspicuousness (Zahavi, 1975), or examine their feathers' margins for evaluating wear and tear as a cue for the male general quality, or use feather decorations such as contour lines at the feathers' margins to improve the perception of wear and tear (Hasson, 1991a). In the first case females respond to x alone, in the second, to Q alone (no signal is involved, hence $\hat{x} = x_0$), and in the third, to the interactions between x and Q : the more elaborate the feather contour lines, the better can be the perception of the feathers' wear and tear, hence of the male quality. Consequently, it should be recognized that S can be a function of both the signaler's Q and x .

The second step requires the breakdown of quality into three distinct components. This is because frequently, recipients are not interested in the

signaler's overall quality, but in only a certain, specific component of quality. For example, in a combat, males may need information about their rivals' immediate strength, stamina and agility, but not in their resistance to parasites. In contrast, where males provide no parental care females should show interest in cues that reflect the male genetic quality, such as tail length or antler size, which are not sensitive to little fluctuations in condition. Similarly, pollinators may be interested in the flower's pollen or nectar crop, but not in the plant's defense against herbivores (although these may correlate).

The specific quality (or qualities) that is sought by recipients is denoted here by Q_s . Assuming that natural selection acts to increase the precision of a recipients' response then, by definition, recipients are selected to respond to variations in the signalers' Q_s . Q_s becomes a function of x only if the signal "uses up" this specific quality (for example, if money is advertised by spending money, or escaping potential by decreasing flight distance). Fitness components other than Q_s , upon which "general" costs are imposed as a consequence of the evolution or the maintenance of a signal, are denoted by Q_G , whereas Q_F denotes all other fitness components that are not affected by the signal. Consequently, eqn (2) converts to:

$$W = G\{F[Q_F, Q_G(x), Q_s(x)], S[Q_s(x), E, x]\}. \quad (3)$$

This division of quality is the key to the understanding of signal design, as I show below in some detail.

2.4. THE SIGNALER'S NEEDS

To improve their fitness, individuals have to fulfil needs for certain resources that are sometimes controlled by other individuals, such as food, water, protection and sex. Much of the communication between offspring and parents is probably based on the advertisement of the offspring's needs (Trivers, 1974; Godfray, 1995). Like quality, needs represent a component that is part of the signaler's features, and have an effect on both F and S . Although needs and quality may sometimes be negatively correlated with each other (Godfray, 1991), at other times they are generally independent. As a general rule, needs are determined by short-term fluctuations in variables that determine basic potential fitness, whereas quality represents variables that persist longer and usually show only gradual changes (even injuries, which result in sudden changes in quality, may only gradually recover). As I show below, the nature of signaling need and quality is expected to be qualitatively different. I also show that, in contrast with quality, it is highly unlikely that needs are a function of x . By

denoting needs with N , eqn (3) becomes:

$$W = G\{F[Q_F, Q_G(x), Q_s(x), N], S[Q_s(x), E, x]\}. \quad (4)$$

Because needs represent short term fluctuations, they cannot usually be perceived independently of Q_s . Hence the benefit function, S , is not a direct function of N (although, at equilibrium, x is expected to be correlated with N). I explain this further below.

2.5. CHOICE-BASED ENVIRONMENTS: ATTRACTION AND DETERRENCE

In many biological systems, interactors are clearly divided into selecting and selected parties, and hence were termed "choice-based" systems (Hasson, 1994). Due to the nature of interactions between the selecting and the selected parties, choice-based environments are divided into two system types: systems of attraction (females select among males and/or vice versa, parents among their offspring, pollinators among flowers), and systems of deterrence (predators select prey, rivals select rivals). Members of the selected party benefit from attracting selectors in systems of attraction, and deterring or avoiding selectors in systems of deterrence (Hasson, 1994). Signals that selectors produce are aimed to fit this goal. S and Q_G of some signals ("recognition" signals, see below) apparently are sensitive to the type of the choice system in which the signaler and recipient interact. By denoting with C the dichotomous variable that describes the type of the choice-based environment (either attraction or deterrence system), we derive the most general equation that represents a signaler's fitness:

$$W = G\{F[Q_F, Q_G(C, x), Q_s(x), N], S[Q_s(x), E, C, x]\}. \quad (5)$$

By showing that all signal types can be represented by simple derivations of this equation (Table 1) and how this model (its notations, equations, assumptions and conclusions) helps in identifying selective regimes operating on signals, I demonstrate both the model's generality and usefulness. Table 2 should be used as a non-formal guide to the different signal types.

3. Activators and Pointers

A very useful terminology of signals that will be used throughout this paper arises from the often overlooked recognition that signals can function as "activators" or as "pointers". Each of these two options has a qualitatively different effect on the signalers' S . I define pure activators as signals that elicit recipients' response regardless of environmental factors (E) or the signaler's actual needs (N) or underlying quality (Q_s). Consequently, S of signalers

of activators is not a function of E and Q_s , and recipients respond only to x . This type of signals corresponds with Dawkins & Krebs' (1978) view of actors (signalers) and reactors (recipients), hence their name. Unlike Dawkins & Krebs' view of signals, however, this definition is neutral with respect to the signals' reliability; activators may or may not be reliable.

In contrast to activators, I define pure pointers as signals that direct (or divert) attention to (from) other cues or signals that are correlated with the signaler's Q_s or with other facts or events, E . Hence, S of signalers that use pointers is a function of either both x and Q , or both x and E . Some signal types are only activators, some are only pointers, and some may be pure activators, pure pointers or a mixture of both. For example, a long attractive tail is an

activator, a feather contour line that draws attention to the feathers' wear and tear is a pointer, and a warning signal aimed at conspecifics may function as either one or as both simultaneously (giving an "instruction" to hide by eliciting an unconditional hiding response, pointing at a predator's presence, or doing both). This is explained below, as I discuss each signal type.

4. Choice-based Environments

The primary classification of signals (capital letters in Tables 1, 2) relates to the general "environment" that determines selective forces that lead to the evolution of signals. The choice-based environment is different from the other two environments in that signals evolve in an environment that is based on

TABLE 1
The effect of the different signal types on the signaler's fitness

The general model: Assumptions: Eqn (5): Properties:	$\partial F/\partial x < 0, \partial S/\partial x > 0$ $W = G\{F[Q_F, Q_G(C, x), Q_s(x), N], S[Q_s(x), E, C, x]\}$ $\dot{x} > x_0$
A. Choice-based environments: Assumptions: Eqn (6):	$\partial S/\partial E = 0$ $W = G\{F[Q_F, Q_G(C, x), Q_s(x), N], S[Q_s(x), C, x]\}$
(1) Assessment signals: Assumptions:	$\partial S/\partial N, \partial F/\partial N, \partial S/\partial C, \partial F/\partial C = 0$
(a) Activating assessment signals: Assumptions: Eqn (8):	$\partial S/\partial Q_s = 0$ $W = G\{F[Q_F, Q_G(x), Q_s(x)], S[x]\}$
(i) <i>Quality handicaps, bluffs</i> : Assumptions Eqn (8): Properties:	$\partial F/\partial Q_s > 0$ $W = G\{F[Q_F, Q_G(x), Q_s(x)], S[x]\}$ $\partial \dot{x}/\partial Q_s > 0$
(ii) <i>Pure attractors or repellents</i> : Assumptions: Eqn (11) and (12): Properties:	$Q_s = 0$ or $\partial Q_G/\partial x \approx 0$ $W = G\{F[Q_F, Q_G(x)], S[x]\}$ or $W = G\{F[Q_F], S[x]\}$ $\partial \dot{x}/\partial Q_s = 0$ $\partial S/\partial Q_s \neq 0$
(b) Pointing assessment signals: Assumptions: Eqn (7):	$W = G\{F[Q_F, Q_G(x), Q_s(x)], S[Q_s(x), x]\}$ $\partial S/\partial Q_s > 0$
(i) <i>Amplifiers</i> : Assumptions Eqn (7):	$\partial S/\partial x > 0$ for high Q_s , $\partial S/\partial x < 0$ for low Q_s $W = G\{F[Q_F, Q_G(x), Q_s(x)], S[Q_s(x), x]\}$ $\partial S/\partial Q_s < 0$
(ii) <i>Attenuators</i> : Assumptions: Eqn (7):	$\partial S/\partial x > 0$ for low Q_s , $\partial S/\partial x < 0$ for high Q_s $W = G\{F[Q_F, Q_G(x), Q_s(x)], S[Q_s(x), x]\}$ $\partial S/\partial Q_s > 0$
(iii) <i>Indices</i> : Assumptions: Eqn (7):	$\partial S/\partial x > 0$ (always) $W = G\{F[Q_F, Q_G(x), Q_s(x)], S[Q_s(x), x]\}$ $\partial S/\partial Q_s, \partial S/\partial E = 0$ $C = \text{attraction}$ $W = G\{F[Q_F, Q_G(x), N], S[x]\}$
(c) Signals of need: Assumptions: Eqn (14):	$\partial F/\partial Q_s, \partial F/\partial N = 0$ $W = G\{F[Q_F, Q_G(C, x)], S[Q_s(x), C, x]\}$
(i) <i>General handicaps</i>	$Q_s = \text{constant}$ $W = G\{F[Q_F, Q_G(C, x)], S[C, x]\}$
(2) Recognition signals: Assumptions: Eqn (15):	$Q_s = 0$ or $Q_s = 1$ $W = G\{F[Q_F, Q_G(C, x)], S[Q_s(x), C, x]\}$
(a) Camouflage, Attention signals: Assumptions: Eqn (16):	
(b) Mimicry, Identity signals: Assumptions: Eqn (17):	
B. Cooperation environments: Assumptions: Eqn (18):	$Q_s = 0, \partial F/\partial N, \partial F/\partial C, \partial S/\partial C = 0$ $W = G\{F[Q_F, Q_G(x)], S[E, x]\}$
(a) Symbols & Icons, Lies	
C. Cue-reading environments: Assumptions: Eqn (18):	$Q_s = 0, \partial F/\partial N, \partial F/\partial C, \partial S/\partial C = 0$ $W = G\{F[Q_F, Q_G(x)], S[E, x]\}$
(a) Deceptions	

TABLE 2
A key to the different signal types

Condition	Signal type or environment	Options/examples
A. At least one of the interactors can make a choice of partners (either among existing partners or between existing and future partners). Signalers evolve signals to alter this choice in their own favor, or selectors, to improve their capacity to make such a choice.	Choice environment	If false choose between B and C; if true choose between options A1 and A2.
A.1. Signals are given by the selected party only. They are competitive in the sense that they are used to alter the selectors' choice in favor of the signaler at the expense of other, equally ranked members of the selected party ¹ .	Assessment signals	Options: A.1.a,b,c
A.1.a. Selectors responds to the signal's presence or expression only	Activating assessment signals	Options: A.1.a.i,ii
A.1.a.i. Signals are costly in the sense that poor quality signalers pay a great relative cost. At evolutionary equilibrium the signal's expression is an indicator of the signaler's quality that is sought by selectors.	<i>Quality handicaps</i> ²	Duration of male song; the peacock's train.
A.1.a.ii. Signals are not correlated with any quality that is important to recipients other than the signal itself.	<i>Purely attractive or repellent signals</i>	Signals that are based on sensory biases; Fisherian sexual signals.
A.1.b. Signals improve or diminish the perception of cues or other signals that are used for making a choice.	Pointing assessment signals	Options: A.1.b.i,ii,iii
A.1.b.i. Signals improve perception of the signaler's quality handicaps or cues; only high quality signalers benefit by improving perception of real quality.	<i>Amplifiers</i>	Feather contour lines; behavioral displays that expose morphological features; markers for individual identity.
A.1.b.ii. Signals diminish perception of the signaler's quality handicap or cues: only poor quality signalers benefit by hiding their real quality.	<i>Attenuators</i>	Behavioral displays that attract attention away from injuries or damaged coat; decreased color contrast between flowers' pollen and petals.
A.1.b.iii. The structure of the signal is linked with quality such that avoiding signaling is perceived as poor quality.	<i>Indices</i>	Tiger's high scratching; threat by erection of fur or feathers.
A.1.c. Signals are given in an attraction choice-based environment to indicate the signaler's need for a certain resource (food, defense etc). There must be a mutual interest between the signal recipient (donor), who controls this resource, and the signaler (beneficiary).	Signals of need	Option: A.1.c.i
A.1.c.i. Signals entail cost. At equilibrium their expression is correlated with the signaler's need rather than quality.	<i>General handicaps</i> ²	Nestlings' high posture begging behavior.
A.2. Signals evolve to improve or diminish the perception of the signaler's presence or identity. Many of them may be used by both selectors and the selected party (e.g. predators and prey).	Recognition signals	Options: A.2.a,b
A.2.a. Signals hide or expose the presence of the signaler.	<i>Camouflage, attention signals</i>	Territorial songs ³
A.2.b. Signals enhance or diminish recognition of "legitimate" interactors.	<i>Mimicry, identity signals</i>	Batesian mimicry, Markers for species/sex identity.
B. Costs of signals are often negligible, information is often about characteristics not related to quality or need.	Cooperative environment: <i>Symbols, icons, lies</i>	Human language ⁴ ; the honey bee's dance.
C. Signals are a change in the context in which signalers expose their own characteristics (signals or cues) that are used by recipients as cues for making inferences about the environment.	Cue reading environment, <i>Deception</i>	Feigning injury; false pursuit-deterrent signals.

¹"Equally ranked" from the selector's point of view, which means that in some systems, such as predator-prey, signalers may compete with individuals of other species as well.

²To simplify the definition, I have excluded bluffs used by signalers that are relieved from constraints found in other signalers. When considering, however, only signalers that are equally relieved from such constraints, bluffs behave like handicaps.

³Possibly many short and infrequent territorial bird songs function as attention signals (reminders of the presence of the territory holder).

⁴This should not be confused with a clever use of words, which often serves, for example, to attract mates. In such a case, the way we use words is an amplifier or an index of education, intelligence and character, despite the fact that the words themselves remain symbols.

choice. The interactors, which are the signalers and recipients, belong to two parties, where members of one select their partners among members of the other. Signals in these systems are designed to change information regarding those features of the signaler (Q_s or N) that are sought by recipients. Choice may also be based on the assessment of signals that are pure attractors (e.g. Fisher traits: Fisher, 1930; Lande, 1981; Kirkpatrick, 1982) or repellents, which are not correlated or associated with any quality or need. Based on the estimated relative values of these variables, recipients choose whether to interact with the signaler (or potential signaler, if it chooses not to signal). In contrast, signals in other selection regimes change information about other, external factors (E). This difference results in different signal types, as a result of the different parameters that affect the signalers' F and S functions (Table 1).

Because choice in choice-based environments is based entirely on the potential signaler's own features (Q_s , N and/or x), information about other facts or events (E) is irrelevant and, consequently, the signaler's fitness is expressed by:

$$W = G\{F[Q_F, Q_G(C, x), Q_S(x), N], S[Q_S(x), C, x]\}. \quad (6)$$

Signals in choice-based environments (either attraction or deterrence) are divided into three categories. The criterion for this division is the signaler's feature upon which the recipient's information is changed by the signal. Each of the three different effects on the recipient's information is unique with respect to the parameters that affect S , meaning that there are at least three different major ways (not counting subcategories) by which the signal's specific benefit is gained. Following the order of signaling categories discussed below, the first is "assessment signals", which are used by selectors to assess the signaler's phenotype [here I follow Maynard Smith & Harper, (1995)]. The only reason I hesitate from calling them "quality signals" is the possibility that some assessment signals are purely attractive or purely repellent, even if these are likely to be evolutionarily unstable (see below). Sometimes, however, I use the term "quality signals" to specifically exclude the purely attractive or repellent signals. Hence, quality signals evolve because selectors choose a "partner" among members of the selected party, based on the value of its quality. They are given by members of the selected party because they change the selectors' estimate of Q_s .

The second signaling category in choice-based environments is signals of need which selectors (here, donors) use to select an interactor (beneficiary). In this sense, both assessment signals and signals of need

are competitive, although signals of need exist only in systems of attraction (signalers compete to be selected), whereas assessment signals are found also in systems of deterrence (where signalers compete to be avoided).

The third category in the choice-based environment is recognition signals (such as camouflage and mimicry, or signals of identity), which change the recipient's information regarding its interactor's presence or identity. In contrast with assessment signals and signals of need (which are only given by the selected party to change the selector's information), information regarding their interactor's presence or identity is required by both selectors and members of the selected party. Hence, unlike the former two categories, identity signals can be used by selectors as well as by members of selected parties.

Note that in Hasson (1994), I used the term "choice-based systems" to classify signals, whereas here I only use it to identify a certain environment in which many signals evolve. This helps identifying, whenever it matters, the two possible variable states of this environment, attraction or deterrence, denoted by C . Signals in choice environments, namely, assessment signals, signals of need and recognition signals, all gain their specific benefit from their potential to change the recipient's decision of whether to interact with the signaler. However, the first two assume recognition and are based on competition between "legitimate" members of the selected party for favors given by selectors (in attraction systems) or for minimizing costs as a result of interactions with selectors (in deterrence systems). In contrast, recognition signals change information regarding the presence or identification of the "legitimate" interactors to both parties.

4.1. ASSESSMENT SIGNALS

In systems of attraction, such as sexual selection, pollination, or offspring-parent communication, individuals in the selected party benefit by being selected, and evolve signals to attract selectors. In systems of deterrence, such as prey-predator or rivals, the selected party benefits by deterring selectors. Pursuit-deterrent and threat signals, correspondingly, are aimed at this goal. It appears that in both systems, high-quality signalers benefit by advertising their true quality: in attraction systems because selectors benefit by preferring them, in deterrence systems because selectors benefit by diverting their attack to other individuals, specifically, those of poorer quality (Hasson, 1994). Consequently, the type of the choice environment, C , has no effect on either S or F . Also,

assessment signals are not affected by the signaler's needs, hence the signaler's fitness becomes:

$$W = G\{F[Q_F, Q_G(x), Q_S(x)], S[Q_S(x), x]\}. \quad (7)$$

The competitive nature of assessment signals is a consequence of competition between signalers for favors given by selectors in systems of attraction, and for reduced losses from interactions with selectors in systems of deterrence.

4.2. ACTIVATING ASSESSMENT SIGNALS

Assessment signals are either pure pointers, where Q_S and x interact, or pure activators, where choice is based on x only. For activators, if a signaler's quality is perceived, it is perceived only through the signal intensity, x . Thus, Q_S has no effect on the signaler's S , and its fitness is described by:

$$W = G\{F[Q_F, Q_S(x), Q_G(x)], S[x]\}. \quad (8)$$

Handicaps and bluffs

Equation (8) can take on different specific functions for G , F and S (see Nur & Hasson, 1984). In explicit models of sexual selection (e.g. Maynard Smith, 1976, 1985; Lande, 1981; Andersson, 1982; Kirkpatrick, 1982; Nur & Hasson, 1984; Pomiankowski, 1988; Michod & Hasson, 1990), eqn (8) is usually assumed to take the more specific form of:

$$W = Q_S(x) \cdot S(x), \quad (9)$$

where $F = Q_S(x)$ represents male survivorship (all fitness components, with the exception of mating success described by $S(x)$, are assumed to be implemented in survivorship; hence, no separate Q_F or Q_G are required). For most biologically reasonable functions of F and S (subject to $\partial F/\partial Q_S > 0$, $\partial F/\partial x < 0$, $dS/dx > 0$), eqn (9) describes a hump-shaped function with a maximum at \hat{x} , where \hat{x} is positively correlated with Q_S (Nur & Hasson, 1984).

Equation (9) describes a special case of a handicap, which we can characterize by three elements:

- (1) Handicaps are quality signals that are also activators, hence they are fully described by eqn (8).
- (2) F and S in eqn (8) are subject to $\partial F/\partial Q_S > 0$, $\partial F/\partial x < 0$ and $dS/dx > 0$.
- (3) $\partial \hat{x}/\partial Q_S > 0$, at least within the biologically meaningful range of parameters values.

The reliability of the handicap is described by element 3 whereas the mechanism that maintains reliability as a result of the trade-off relationships between the signal's costs and benefits, is described by element 2. Differential F components ($\partial F/\partial Q_S > 0$) ensure that at equilibrium the signal expression is a function of the quality sought by recipients (element 3). This is achieved for any x value (a) as long as for any given x the slopes of decreasing F of all Q_S 's, as a function of x , are equal, or (b) if those slopes decrease faster for individuals with lower Q_S (Nur & Hasson, 1984). The second option is often termed the differential costs (Pomiankowski, 1988; Grafen, 1990). $\partial F/\partial Q_S > 0$ is, therefore, the heart of the handicap mechanism, and may be verbally referred to as "differential relative costs" (differential costs are sufficient for resulting in the handicap reliability, but not necessary; differential relative costs are both sufficient and necessary). Its biological interpretation refers to the requirement that for any signal intensity, the signaler's basic fitness component, F , is higher for a higher value of its specific quality that is sought by recipients.

The correlation between \hat{x} and Q_S becomes less tight if Q_S and Q_G are not correlated with each other. In such a case, the more moderate the slope of $\partial Q_S/\partial x$ and the steeper the slope of $\partial Q_G/\partial x$ (i.e. the negative effect of the signal on its carrier's F becomes weaker *via* Q_S than it is *via* Q_G), the less reliable is a handicap in advertising Q_S . This is because differences in \hat{x}

TABLE 3
The signaler's fitness using ideal signals

Signals	Equation
Quality handicaps and bluffs (10)	$W = G\{F[Q_F, Q_S(x)], S[x]\}$
Pure attractors or repellents (12)	$W = G\{F[Q_F], S[x]\}$
Amplifiers (13)	$W = G\{F[Q_F], S[Q_S(x), x]\}$
Attenuators (13)	$W = G\{F[Q_F], S[Q_S(x), x]\}$
Indices (13)	$W = G\{F[Q_F], S[Q_S(x), x]\}$
General handicaps (14)	$W = G\{F[Q_F, Q_G(x), N], S[x]\}$
Camouflage, attention signals	$W = G\{F[Q_F], S[C, x]\}$
Mimicry, identity signals	$W = G\{F[Q_F], S[Q_S(x), C, x]\}$
Symbols & icons, lies	$W = G\{F[Q_F], S[E, x]\}$
Deceptions	$W = G\{F[Q_F], S[E, x]\}$

NB. Reference to equations of ideal signals that are found in the text is given in parentheses.

increasingly reflect differences in Q_G rather than in Q_S . Hence, ideally, if a handicap is aimed at being perfectly reliable, it should be designed such that the only cost paid is expressed in units of the quality sought by selectors, Q_S . Therefore, an ideal handicap is described by:

$$W = G\{F[Q_F, Q_S(x)], S[x]\}, \quad (10)$$

(See Table 3). Typical models of handicaps in sexual selection [eqn (9)] thus represent the special case of an ideal handicap by making the assumption that x decreases viability only, which is also the quality sought by females. Similarly, flight distance of an alert prey (the shorter the distance the greater the x and the accompanied risk) may function as an ideal handicap advertising the prey's escape potential (here, Q_S). This is because the probability of escaping decreases as the distance from predators decreases, while other prey qualities are unaffected (Hasson, 1991b; Vega-Redondo & Hasson, 1993). Thus, the concept of ideal handicaps is important because it enables a better understanding of signal design and signal specialization. The notion of an ideal handicap could be useful here for making a generalization: I define "ideal signals" as signals whose specific effect, the effect that is unique to each signal type, is perfected such that the signals induce no side effects on the signalers' fitness, which may only inhibit their evolution (Table 3).

Bluffs are defined in Hasson (1994) as costly signals expressed by individuals whose quality is relatively poor. At equilibrium, they are expressed only by those individuals who are, for whatever reasons, relieved of some of the constraints shared by other signalers (for example, stags in their last reproductive season need not reserve resources for further survival and may increase their investment in antlers relative to other males of similar quality). When compared to similarly constraint-free individuals, however, bluffs are nevertheless trapped by the handicap mechanism, which means that their \hat{x} must correlate with their Q_S (Hasson, 1994). Equation (8) is thus as appropriate for bluffs as it is for handicaps (Table 1).

Pure attractors or repellents

Unlike a handicap, whose expression functions as a quality indicator, a pure attractor or repellent points at no underlying quality. Hence, no specific quality with an effect on the signal evolution is pursued by selectors. This is mathematically expressed by setting $Q_S = 0$. This is the case, for example, where no variation in quality exists among members of the selected party. This case is represented by:

$$W = G\{F[Q_F, Q_G(x)], S[x]\}. \quad (11)$$

A second possibility, which may represent an ideal case of pure attractors and repellents, is where signals do not entail any significant cost (i.e. $\partial Q_G/\partial x \approx 0$ throughout the available range of x values). This may be found, for example, where costs imposed on a handicap are suddenly removed (say, by invasion into a new, predator-free habitat). This case is represented by:

$$W = G\{F[Q_F], S[x]\}. \quad (12)$$

Either of these two options leads to $\partial \hat{x}/\partial Q = 0$ (Table 1). Because they provide no information on the signaler's quality, the classification of pure attractors and repellents as cheating signals (Hasson, 1994) is justified. Because selectors do not direct benefit by responding to them, the evolution or maintenance of selectors' response to pure attractors or repellents depends on the intensity and stability of non-selective forces such as linkage disequilibrium (Fisher, 1930; followed by explicit models by Lande, 1981; Kirkpatrick, 1982) or sensory exploitation (Ryan & Keddy-Hector, 1992), none of which are evolutionarily stable (Michod & Hasson, 1990; Hasson, 1994).

4.3. POINTING ASSESSMENT SIGNALS

Assessment signals that are pointers are divided into (a) an antagonistic pair of signals, amplifiers and attenuators, and (b) indices. These signals are distinguished by their different effects on their carrier's S .

Amplifiers

Amplifiers are described by eqn (7), and characterized by

- (1) $\partial S/\partial Q_S > 0$,
- (2) $\partial S/\partial x > 0$ if Q_S is sufficiently high, and
- (3) $\partial S/\partial x < 0$ if Q_S is sufficiently low.

These relationships describe a state in which the signal improves the perception of another signal or cue that is correlated with the signaler's Q_S . For example, many behavioral displays, such as the fanning of the peacock train, parallel walking or swimming, etc, improve perception of size and condition of feathers, fur or fins. Consequently, big signalers in good condition benefit, whereas signalers that are small or in poor condition lose by revealing their quality. Similarly, if orientation of a potential prey's ears points at the focus of its attention, then conspicuous markings at the ear tips or margins improve the predator's perception of the prey's alertness. Alert prey should benefit, while the chances that a predator stalks and hunts non-alert prey,

should increase (Hasson, 1989, 1991a, b; Hasson *et al.*, 1992).

The initial perception of quality is described by $\partial S/\partial Q_S > 0$ (element 1), at $x = x_0$. As x increases, the differential response of selectors to the signaler's Q_S is further amplified (elements 2 and 3): high rewards to high quality signalers further increase, low rewards to poor quality signalers further decrease. One can easily see from this that the fitness of the average signaler, and hence the evolution of amplifiers, depends on the frequency of high *versus* low quality signalers, unless low quality individuals drop signaling altogether (see explicit models by Hasson, 1989, 1990; Hasson *et al.*, 1992).

In contrast with the “trade-off” reliability of handicaps, amplifiers are reliable by design. This means that certain signal patterns increase perception of quality, hence the signal reliability, better than others (Hasson, 1991a). Thus, amplifiers need not be costly in terms of either Q_S or Q_G , to be reliable. In fact, ideally (Table 3), amplifiers are cost free and described by:

$$W = G\{F[Q_F], S[Q_S(x), x]\}. \quad (13)$$

At equilibrium, amplifiers may be indicators of quality ($\partial \hat{x}/\partial Q_S > 0$) (Hasson, 1990, 1991a). Unlike handicaps, however, this is not a necessary feature of amplifiers. Furthermore, if amplifiers become indicators of quality, this is the result of differential benefits (elements 2 and 3), as a result of reliability by design, not differential relative costs. Where $\partial \hat{x}/\partial Q_S > 0$, selectors may switch to using x as a quality indicator, in addition to the original cue that is further amplified by x . If x further evolves as a result, while increasing costs on Q_S , then at equilibrium the signal may become a mixed signal and function as both an amplifier and a handicap (Hasson, 1990).

Attenuators

Whereas amplifiers expose cues or signals that reveal quality, attenuators hide them. For example, non-glossy uniform feather colors decrease perception of individual feathers, and hence of their wear and tear. Similarly, by converging pollen and petals colorations, a plant can conceal pollen that could have fallen as a result of previous pollinators' visits, thereby hiding information about the flower's nectar. Consequently, differences in S , based on previously perceived variations in Q_S at the point $x = x_0$, are attenuated. This benefits (increases the S of) individuals with low Q_S , and harms signalers with high Q_S . Thus, the effect of attenuators on the signaler's S is the exact opposite of that of amplifiers. However, because, by definition, both amplifiers and

attenuators may decrease F (via either Q_S or Q_G), the elimination of one may not necessarily be identical to the evolution of the other (Hasson *et al.*, 1992).

Like amplifiers, attenuators gain their specific benefit ($\partial S/\partial x > 0$) by their special design, although they are cheating signals. Their signaler's fitness is described by eqn (7), and their evolution is similar to that of amplifiers except that the inequality signs in elements 1, 2 and 3 are reversed. Consequently, they evolve with different parameter values. Unlike amplifiers, if a cost is paid in Q_G when Q_S and Q_G are correlated, or when the cost is paid in units of Q_S , there are conflicting tendencies in F and S in optimizing the degree of attenuation with respect to Q_S . As a result, the attenuator's intensity may not be always negatively correlated with Q_S , a fact that may affect the stability of S .

Indices

Semiotic theory defines an index as a sign (either a cue or signal) that has a factual connection with the thing signified, such as animal tracks, droppings, etc (Peirce, 1965–7). Maynard Smith & Harper (1995) use this term for “signals that are physically associated with a quality of interest to the receiver” (i.e. Q_S). They nicely illustrate this with an example of a tiger scratching tree trunks as high as it can, thereby giving an index that reliably advertises its size. The very same principle may also hold for the territory marking by the male dog who raises his hind leg to urinate. Similarly, a cat arching its back or erecting its fur to threaten its enemy may also give an index of its size. Like other signalers of indices, the cat cannot give a better signal (i.e. appear bigger than its maximum stretched size) while, regardless of its size, it always does worse if it does not signal because it then appears smaller. Thus, following Maynard Smith and Harper's definition, indices are characterized by:

- (1) $\partial S/\partial Q_S > 0$.
- (2) $\partial S/\partial x > 0$; in contrast to amplifiers, this applies to all Q_S 's.

Indices are also described by eqn (7) and, ideally (Table 3), like amplifiers and attenuators, indices are cost free and are described by eqn (13). Indices are reliable by design and, unlike amplifiers, benefit all signalers (element 2, above). Therefore, their evolution is not frequency dependent, and should occur whenever signalers are capable of producing them because selectors should not change their choice criteria as indices evolve. At equilibrium, x is only constrained by the signaler's physiology or morphology.

4.4. SIGNALS OF NEED

Signals of need, such as nestlings begging behavior, are parallel to quality signals in that a selector is often making a choice among several simultaneous signalers, or evaluates its interactions with each separately in time or space, based on a certain signaler feature, here the signaler's need. In parallel to the relationships between quality signals and quality, signals of need can only evolve if the advantage to the donor of interactions with the signaler increases as the signaler's need increases. It is different, however, in that the signal recipient is a donor who benefits the signaler while committing a seemingly altruistic act (if we ignore inclusive fitness calculations). Superficially, the mutual interest of signaler and recipient to preserve the former makes such signaling systems resemble the "co-operative environment" (see below), which leads to arbitrary, cost-free signals. However, these two systems differ in the way potential conflicts between signalers and recipients are resolved. While in co-operative environments (leading to arbitrary, cost free symbols) conflicts are resolved by an investment made by recipients to verify the alleged information (see below), potential conflicts are resolved in signals of need by an investment made by the signaler, namely an increase in the signals' costs. A general simple game theory model, entitled "the Sir Philip Sidney game", introduced and analysed by Maynard Smith (1991b, 1994) is enlightening.

Maynard Smith's motivation for introducing the Sir Philip Sidney game was to present Grafen's handicap model (Grafen, 1990) in a simple, tractable model (Maynard Smith 1991b, 1994). The model describes a donor (Sir Philip Sidney) and a beneficiary (a soldier), where the donor may choose to give a resource (a water bottle) to the (thirsty) beneficiary, or choose not to do so. Both benefit by keeping the resource, and the only reason the donor is inclined to help the beneficiary is because he somehow benefits by saving the beneficiary, say, if they are related. The donor has no information of the beneficiary's need except through a signal given by the latter. Based on the terminology we have developed above we can say that such a signal can only be a pure activator. There is only partial agreement between the donor and the signaler: sometimes the interests of the donor and beneficiary conflict, and the beneficiary may be interested in receiving more than the donor is willing to give.

Maynard Smith analysed a no conflict state that will be discussed in Section 5, below, which deals with symbols. He also analysed the state where there is a conflict of interests between the donor and the

beneficiary. The assumption is that the donor cannot identify the beneficiary's need, thus cannot make the distinction between cases of conflict and cases where interests overlap. The model's conclusion is that an (honest) signal of need is stable only if it is costly. Where does this cost come from? Maynard Smith is not specific, but we must assume that the cost is in Q_G . In other words, this is a general cost, not a cost paid in units of thirst (N). In fact, signals cannot be in units of thirst because this will mean that the signaler (here, soldier) will be less thirsty after it signals. Hence, N is not a function of x . Because choice here is not based on the signaler's quality, Q_S is irrelevant to the evolution of signals of need. Also, S is determined by the signal only, and the choice environment in which signals of need are found is always attraction, hence C is constant and irrelevant to the evolution of signals of need. Consequently, the signaler's fitness is described by:

$$W = G\{F[Q_F, Q_G(x), N], S[x]\}. \quad (14)$$

Is this a model of a handicap? In the sense that a signal must be costly to maintain its reliability, the answer is definitely yes. The empirical evidence that shows a positive correlation between the degree of need for parental care and signaling (e.g. Weary & Fraser, 1995) further supports this claim, although such a correlation may be found by the amplifying mechanism as well (Hasson, 1990, 1991a). However, handicaps of quality are different from handicaps of need in that the latter's costs are not specific. Any general cost will do. The only reason that a general cost nevertheless maintains the signal reliability and stability is because the cost decreases the total gain of signaling, especially for a beneficiary that is not in need. In other words, when signals are costly to produce, those that benefit little from signaling should drop signaling sooner than those that benefit more from it. Because in the Sir Philip Sidney game those that benefit less are also the would-be cheaters, then the greater the costs, the less will be cheaters inclined to signal. The Sir Philip Sidney game is, therefore, not just a simplified version of the handicap model, but also a different one. This difference is also reflected in the expected nature of signals. Quality handicaps are expected, at equilibrium, to specifically handicap qualities sought by recipients whereas, because any general cost maintains the reliability of signals of need, these can be arbitrary. Factors that may prevent them from being entirely arbitrary can only be developmental or phylogenetical constraints, or limits to the proficiency of recipients to perceive differences in some signals, at their optimal signaling values, as a function of the signalers' need.

In order to make a generalization and include the possibility that handicaps of some other signaler features are arbitrary and are similarly based on any (general) cost (see Discussion for possible reasons for the connection between the two), I prefer to use the term “general handicaps”, where handicaps of need are but their special case (even if the only one). Thus, we should make the distinction between general handicaps and quality handicaps, which are different in several respects.

It is worth adding that offspring–parent communication is often a mixture of signals of quality and need (e.g. Kilner, 1995). Depending on their expected yield (grand offspring), parents are expected to select their best offspring (by responding to quality cues and signals) while being sensitive to the needs of each of them.

4.5. RECOGNITION SIGNALS

Recognition signals refer to signals that expose or hide information regarding the identity or presence of signalers, rather than their quality. Unlike assessment signals, which are only given by members of the selected party that compete for the privilege of being selected (in systems of attraction) or rejected (in systems of deterrence), recognition signals may be delivered by selectors as well. Recognition signals are comprised of two pairs of antagonistic signals that are distinct by the nature of information they modify. One pair is camouflage and attention signals, which hide or expose information regarding the signaler’s presence; the other is mimicry and identity signals, which change information with regard to the signaler’s identity. The specific quality desired by recipients of recognition signals is, correspondingly, either the signaler’s presence or identity. Both of these qualities are variables for a recipient but constant to a signaler. Consequently, Q_s may have an effect on the signaler’s S , but not on its F . Correspondingly, for recognition signals the signaler’s fitness is described by

$$W = G\{F[Q_F, Q_G(C, x)], S[Q_s(x), C, x]\}. \quad (15)$$

Camouflage and attention signals

Camouflage and attention signals divert (or attract) the recipients’ attention to (or from) the mere presence of individuals rather than to their quality (Fleishman, 1992; Hasson, 1994). Hence, Q_s reflects only presence or absence of a signaler. Here, Q_s is identical for all individuals (from their own point of view, all signalers exist), so Q_s has no effect on F and S (therefore, camouflage and attention signals are pure activators).

The choice-based “environment” (C) shows an interesting opposing effect on signalers of camouflage and attention signals. Attention signals benefit their carriers through interactions in systems of attraction (e.g. by attracting potential mates), while camouflage signals benefit their carriers through interactions in systems of deterrence (e.g. by avoiding predators or prey). Hence, if x is a measure of the signaler’s conspicuousness, then \hat{x} of an attention signal is determined by maximizing

$$W = G\{F[Q_F, Q_G(C, x)], S[C, x]\}, \quad (16)$$

where Q_G represents the signaler’s qualities upon which costs of attention signals are imposed (the potential to avoid predators or rivals as well as the fitness components upon which costs of producing the signal are imposed), and S represents benefits in attraction systems (e.g. attracting attention of mates).

Camouflage is represented by the same equation except that interactions in deterrence systems are expressed in S as benefits in avoiding predators or rivals, and interactions in attraction systems as costs in F , because signalers may be more difficult to find by selectors, such as potential mates. Other fitness components sacrificed to produce camouflage are also included in Q_G . Therefore, when put together, x becomes a measure of conspicuousness, and C alters the signs of Q_G and S for each “environment”, attraction or deterrence. Optimal conspicuousness, \hat{x} , should be computed by maximizing eqn (16), where S expresses expected benefits in both deterrence and attraction systems, and F , expected costs in these two systems. When $\hat{x} > x_0$, an attention signal is expected, and when $\hat{x} < x_0$, camouflage is expected.

Most signals affect conspicuousness, hence they must induce a component that is either an attention signal or camouflage, which exposes or hides their carriers. Usually, this component should be implemented in other signal types as costs paid in units of Q_G , and sometimes as benefits in S . An interesting special case in which the involvement of attention signals in other signal types becomes the signal’s main effect may be found in sexual selection systems. Suppose that Q_s , the quality sought by selectors (females) is the (male) potential to cope with predators or rivals, as a function of strength, stamina, agility, etc. In such a case, Q_G in eqn (16) is replaced by (Q_s, Q_G) , where Q_G remains the costs of producing conspicuousness only, which is not a function of C . C is implemented in Q_s and S as constants (namely, $C =$ deterrence in F [via its effect on Q_s], and $C =$ attraction in S). Consequently, eqn (16) turns out to be identical to eqn (8) and describes a handicap, where costs of increased conspicuousness

TABLE 4

The effects of the environment ($C = \text{attraction or deterrence}$) and identity ($Q_S = \text{true or false}$) on the sign of the signaler's S

A. When using identity signals:		
	True	False
Attraction	+	+
Deterrence	-	+
B. When using mimicry:		
	True	False
Attraction	-	-
Deterrence	+	-

Q_S is true when identity is the one sought by recipients, and false otherwise. “+” indicates a positive effect on S , and “-” a negative one. Consider, as an example, a male who may give an identity signal or mimicry to a conspecific (if true) or heterospecific (if false) female, as well as to its true predator (if true) or to a predator for which it is an unsuitable prey (if false). Although others examples may be found for which at least some of the signs will be reversed, the strong opposing effects of identity and of the choice-based environment on the sign of S in identity signals and mimicry are evident.

increase risk of predation. If costs of producing conspicuousness are sufficiently small, eqn (16) may be approximated by eqn (10). Attention signals that are cheap to produce may, therefore, constitute ideal handicaps for advertising the signaler's potential to cope with predators or rivals. Ideally (Table 3), camouflage and attention signals should be designed to minimize Q_G by (a) reducing costs of producing the signal, and (b) exploiting different perception mechanisms of selectors in attraction and deterrence systems.

Mimicry and Identity Signals

In addition to errors of misjudged quality, selectors in choice-based systems are susceptible to errors of not properly identifying their legitimate selected parties. Similarly, the selected party often needs to recognize their selectors (predators, rivals, potential mates, etc). This leads to another antagonistic pair of signals: identity signals, which decrease the likelihood of mistaken identity, and mimicry, which increase it. Identity (Q_S), taken from the recipient's point of view, can only be true or false and has no effect on F , but does affect S . Thus, the signaler fitness is described by:

$$W = G\{F[Q_F, Q_G(C, x)], S[Q_S(x), C, x]\}. \quad (17)$$

Mimicry and identity signals are pure activators because recipients respond to them unconditionally, and the signals do not point at any underlying quality (here, identity). Note that signals that improve or

diminish perception of other signals or cues that point at identity are not identity signals or mimicry. Instead, they function as amplifiers or attenuators, correspondingly.

Unlike other pure activators, the S of mimicry and identity signals is a function of identity (Q_S), and benefits or costs crucially depend on whether the signaler is a “legitimate” signaler and whether the system is attraction or deterrence. Each dual option (“legitimate” versus “illegitimate”, attraction versus deterrence) may reverse the sign of S . The signal type itself, mimicry or identity signal, also has an opposite effect on S (Table 4). Whether the signaler is the selector or a member of the selected party does not affect the sign of S . This points at the high complexity of mimicry and identity signals, which are strongly affected by the milieu in which they evolve.

Relative to identity signals, the design of mimicry should be much more complex. This is a result of a strong asymmetry that exists between the two signal types. A good identity signal need only represent a single deviation from perceivable patterns found in illegitimate interactors, whereas mimicry must often include many details (Charlesworth, 1994) to eliminate all the discriminating differences from the legitimate interactors. Consequently, under most circumstances, proper identification of interactors are likely to be a result of the evolution of recognition only (i.e. in recipients rather than in signalers), based on the interactor's already existing characters. These may be cues, or signals such as amplifiers, handicaps, or even camouflage patterns. Consequently, although recognition of identity is probably very important, the role of identity signals in communication may be relatively small.

There is at least one type of identity signal, however, whose design may be rather complex. This is where several signalers converge to produce similar signals, as is the case of Mullerian mimicry. These signals increase resemblance between species, hence they constitute “mimicry” in the taxonomist's eyes. However, Mullerian mimicry increases the distinction between “tasty” and “untasty” prey. From the appetizing point of view of a predator, pure Mullerian mimicry (see Malcolm, 1990) is an identity signal rather than mimicry. Hence, the signaling theory suggests that “Mullerian identity signals” is a more appropriate term than “Mullerian mimicry”.

From an evolutionary perspective, signals that evolve to show identity may not always be attributed to identity signals. A good example is given by Dawkins & Guilford (1991) who argue that signals that enhance individual identity may evolve to increase memorability of performance in previous

fighters. In this case, S functions of individuals with high Q_s (here, fighting ability), who are most likely to have won previous encounters, increase with improved identity (i.e. with x). In contrast, individuals with low Q_s , which are most likely to have lost previous encounters, further decrease their probability of gaining resources by increasing perception of their individual identity, and will probably have to fight harder to improve their status. Hence, although they improve individual recognition, signals of individual identity, by increasing memorability of previous encounters, effectively function as amplifiers of differences in status and fighting ability rather than as identity signals.

5. Cooperation Environments

Sometimes, at least within a certain repeatable context, selecting or being selected is irrelevant to the communicating partners. Instead, they may share an interest in accomplishing a mutual goal. For example, both parents and their young benefit by a warning signal given by the parents when a predator is approaching. This creates a special “environment”, in which both partners benefit by the recipient’s increased information of a certain variable whose state is denoted by E . The signal given by a signaler may change the recipient’s estimate of E in a way that alters the signaler’s S . Here, E does not refer to the signaler’s presence, identity or quality, but to either the state of external events, objects or organisms, expected changes in pay-offs as a result of instructions given by the signaler or, in cases of coordinated actions such as cooperated hunt or parental investment, the signaler’s intentions. Note that I make a distinction between such intentions and intentions that represent a general trend that is correlated with the signaler quality (status, vigor etc.) in choice-based environments, such as a general tendency to escalate in a fight. Information about the latter may be revealed or concealed by quality signals.

The mutual interests of cooperative partners may lead them to evolve signals that are reliable by convention (i.e., only as long as the communicating partners cooperate), such as words in the human language and, probably, also the honeybees’ dance. Released from any requirement to be proven reliable, such signals need only be selected to increase efficiency of transmission. Consequently, they may often be conveyed via inexpensive channels. These signals are, therefore, true conventional signals. In accordance with semiotic theory, such conventional signals may be referred to as symbols (arbitrary signals) or icons (signals that are factually similar to

the thing or process signified; Peirce, 1965–7). From a selective point of view, this distinction makes little difference, except, perhaps, for the scenario that leads to their evolution: it seems likely that the evolution of symbols requires a higher degree of sophistication (such as learning) because symbols need to abruptly emerge (or gradually drift from icons), whereas icons may gradually evolve in co-operative biological systems.

An appropriate response by recipients helps in achieving the mutual goal, and hence improves the signalers’ fitness (by definition, their S component). However, costs in F of symbols and icons are often negligible. Consequently, the signaler’s fitness is expressed by:

$$W = G\{F[Q_F, Q_G(x)], S[E, x]\}, \quad (18)$$

where, frequently, $Q_G(x) \approx 0$. x is often merely true or false, but sometimes investment in a symbol or icon may be continuous if a signaler improves the perception of E by repetition or by investing energy in the signals’ transmission over physical barriers or long distances. The (often) low cost of symbols and icons, and especially their detachment from the source of interest may lead to the evolution of lies, which are the manipulative use of these conventions (Hasson, 1994). This should happen when a signaler benefits by not cooperating. The fitness of a “liar” is also expressed by eqn (18). Consequently, the stability and intensity of the recipients’ response depends on the frequency in which signalers “lie” and the consequences of lies on the recipient’s fitness, as opposed to the frequency of times that symbols and icons are used reliably, and the benefits thereafter.

Dawkins & Guilford (1991) and Guilford & Dawkins (1993) use the term “conventional signals” in a wider context. Some of their examples of conventional signals actually belong to other signal types (signals of individual identity, described above, are but one example), whereas some other examples are probably not signals but artifacts of selection operating on recipients to identify their legitimate interactors (Hasson, 1994).

An interesting feature of symbols and icons, which might be very important to their evolution, is that they may be used as activators, as pointers, or as any combination of the two. For example, an alarm call (implying a predator) may be accepted unconditionally as an instruction to hide. This is likely to be the way young birds and mammals respond to their parents’ alarm calls (mutual benefit is the greatest). Alarm calls may, however, be skeptically accepted, and a recipient may first search for the predator. In this case the alarm call is a pointer (attracting

attention to the predator's presence). Depending on the expected risk and signaler credibility, a recipient's response may be a mixture of belief and skepticism. How a mixed response may be accomplished is nicely illustrated by my own anecdotal observations on the yellow-vented bulbuls (*Pycnonotus xanthopygos*) to a live conspecific bird, used as a bait in a cage (Hasson, 1978). When a particular caged bird was attacked by the territorial pair, it often gave an alarm call. After the first call, the attackers escaped to nearest cover. After the second call, they only looked around for a brief moment before resuming attack, and later, the attackers did not respond at all to the caller's alarm call. Whether alarm calls of the yellow-vented bulbuls evolved as symbols (to warn conspecifics) or pursuit-deterrent signals, is irrelevant to this point. What is relevant is that symbols and icons can be similarly checked by being used, frequently or occasionally, as pointers rather than as activators.

Apparently, the potential of symbols to be used, partly or fully, as pointers, may theoretically explain how symbols evolve or become stable. The Sir Philip Sidney game (Maynard Smith, 1991b, 1994) can be used again for seeing this. For cases in which there is very little or no conflict between the partners, the analyses of this game shows that signals can be practically cost free. The state of low conflict can be indicated by a rarity of lies. As the degree of conflict increases, lies are expected to be more common, and this is likely to destabilize the system. The model shows that this difficulty is resolved if symbols bear some cost, which forces the signalers to signal reliably. However, most symbols in the human language are cost free. Either this is indicative of a low degree of conflict in the human society, or something is missing in the model.

This paradox may be resolved if we change one of the model's assumptions. The Sir Philip Sidney model explicitly assumes that symbols are purely used as activators. However, if signal recipients can perceive reliable cues by investment in gathering information, and if they respond to the signals, at least partly, as pointers (i.e. increasing their tendency to make such an investment because their attention or motivation regarding the topic of interest had increased), symbols can be resistant to higher degrees of conflict. This is because the information that is implied by symbols used as pointers is checked first by recipients. Consequently, on average, recipients to symbols do not pay the full costs of being cheated. This lower risk of being

cheated should reduce the cost of signaling that is required by the Sir Philip Sidney model to maintain an evolutionary stable signaling system. Thus, a modification of the Sir Philip Sidney game that assumes that signals may function as pointers (say, if the tendency of Sir Philip Sidney to check the soldier's condition before giving him water increases as a result of the soldier's signals) is likely to show that the higher the frequency of use of symbols as pointers, the lower the threshold of signaling cost. This points to an important conclusion of this suggestion, namely, that symbols and symbolic languages may not be as notoriously cheatable as we have previously assumed.

6. Cue-reading Environments

Organisms respond to various cues in their surroundings, including those found in other organisms. This creates an environment that may lead to deception, if an individual uses such cues to manipulate the behavior of others for its own benefit. For example, signs of injury should be frequently used by predators as cues for prey that is easy to catch. The feigning injury behavior that is used by some birds to lure predators away from their offspring uses this prior predator conception to deceive their enemies. The fitness of signalers that use deceptions is described by eqn (18), where the signal, x , describes the shift in the (manipulative) use of these cues, which induces costs in F . The signaler quality is irrelevant to the evolution of deception; so is the choice-based environment, C . Deceptions are discussed in some detail in Hasson (1994). If recipients respond to deceptions unconditionally, deceptions act as activators. If recipients are suspicious, however, deceptions may be used as pointers.

7. Discussion

I have constructed this model by formalizing first a general definition of signals published elsewhere (Hasson, 1994). I then characterized each signal type by a set of variables that affect its carrier's fitness and by the unique relationships among these variables that result in its evolution. The complexity of the model (Table 1) only reflects the complexity of characteristics that we would like to put under the umbrella of "communication". Despite this complexity, all signals share the basic structure of eqn (1). This indicates that eqn (1) is a useful formal representation of signals as traits whose specific benefit is gained by changing the behavior of others. The recipient's behavioral change usually makes sense if their

information state has changed as a result of signaling (Hasson, 1994; Maynard Smith & Harper, 1995).

This model only describes pure signals: those that are explained by a single evolutionary mechanism. The mathematical derivations of different signal types and the underlying assumptions or characteristics described in Table 1 make an explicit distinction between the different signal types. The different effects that different signals have on the signaler's fitness indicate that signals evolve by a variety of evolutionary mechanisms.

I do not imagine I have described all signal types. The signals discussed here only represent the current general understanding of communication and signaling. I have corrected this model too many times to be convinced that it is complete or fully satisfying. For example, I have only briefly discussed the recipient information state regarding the signaler's motivations and intentions, or the signals that may evolve in order to change them. Greater needs as well as high quality increase motivation. Needs, because they imply a shortage of a resource or resources, and quality (such as body size), because it implies a greater potential to gain or keep resources. Thus, motivation can largely be signaled by signals of need or quality. Can signals of need advertise motivation in deterrence systems, for example, as a component of threat between rivals? Possibly, if the need and quality (specifically, the potential to gain the limited resource) are independent.

Communication about intentions is probably very similar to that of motivations, except that an intention may often be regarded as a tactical immediate action, hence perhaps less predictable than the longer termed motivation.

Another potentially important variable for evaluating benefits and costs of future strategies, at least during fights for limited resources, is the contestants' information state regarding the quality of resources, or their familiarity with the environment. Information about resources affects motivation, and familiarity with the surrounding space can improve fighting skills (Stamps, 1995). Some components of these variables may be advertised by signals of quality. However, it is also possible that some signals are specifically designed to show (or hide) the information state of the signaler, perhaps even using evolutionary routes that are not described here.

It is interesting to find that the design of signals may be arbitrary in two different systems: signals of need and conventional signals (where I specifically mean symbols and icons). It is tempting to put the blame for the resemblance on the mutual interest that exists between signalers and recipients in both

systems. This is misleading, however: when offspring advertise their need, they compete with each other in a way similar to that of signalers of quality. Yet, despite their competitive nature, signals of need are arbitrary, like symbols and unlike quality signals. The important difference between signals of need and quality signals is that quality can be directly perceived by quality cues. The design of quality signals, such as quality handicaps, amplifiers and indices, is often molded by this perception.

In contrast, need, as a rapidly changing state, cannot be perceived and cannot be directly handicapped. Hence, the cost that maintains their reliability is arbitrary, and so is the signal design that is associated with it, the general handicap. Symbols and icons are arbitrary for a similar reason: because they change information about external factors, it becomes impossible to create a linkage between the signal structure and any true information variable.

Signals of need and symbols are qualitatively different, however, in the way they maintain reliability. Signals of need increase reliability by being costly to produce (handicaps), putting the burden of proof on the signaler. In contrast, symbols and icons are more reliable if they are used as pointers. Hence, the burden of proving the signal reliability is on the recipient. By responding to different reliability states of symbols by changing the proportion of their use as pointers rather than as activators, recipients nevertheless benefit from the use of symbols despite their relatively poor inherent reliability. If symbols are too often used as lies, and the subsequent higher cost that is involved in verifying the alleged information as a consequence of signaling becomes greater than the cost of information in the absence of signals, recipients should avoid responding altogether (Hasson, 1994). Hence, some degree of co-operation (i.e. sharing similar goals) is nevertheless required for evolving and maintaining stability of symbols and icons.

The general signaling model points to three methods by which signals may be reliable: (a) by trade-off relationships between F and S (handicaps), (b) by design (amplifiers, indices, identity signals and attention signals), (c) by convention (symbols and icons), sometimes supported by further investigation. Handicaps are reliable as a result of trade-offs between F and S . Handicaps of quality are qualitatively different from handicaps that signal need. To maintain reliability in advertising quality, x must directly affect the quality advertised (Q_S), and minimize general costs (Q_G). The more successful it is in doing so, the more reliable is the signal. To be reliable, a handicap of quality should therefore evolve

to have a very specific design. This contrasts with general handicaps (such as those that advertise need) and points at another difference that is expected between the two: if the Sir Philip Sidney game is a true representative of signals of need (hence, of general handicaps), then different needs can be simultaneously advertised by only a single costly signal.

Ideally, for the second method (reliability by design), signals need not have any effect on Q_s , nor should they affect Q_G (except for unavoidable costs of producing and maintaining the signal). This is the case of amplifiers and indices. It is the special design of amplifiers and indices that increases perception of quality cues and handicaps, and makes them reliable, functional pointers. Ideally (Table 3), signals should be designed to minimize Q_G whenever possible. This is similarly true for the third method of reliability (by convention): symbols do not require any special design to be reliable, except for increasing efficiency of transmission, and being cost free (i.e. minimizing Q_G).

Table 3 nicely emphasizes what is meant by the cost of a handicap as well as the qualitative difference between handicaps of need and quality. The two types of handicaps are the only signals which, ideally, are costly. For quality handicaps this cost is specifically paid in units of Q_s , whereas for general handicaps this cost is just any cost (i.e. paid in Q_G). Another feature of handicaps that makes them different from other reliable signals is that they may only be reliable at equilibrium, where trade-offs between costs and benefits result in $\partial\hat{x}/\partial Q_s > 0$ or $\partial\hat{x}/\partial N > 0$ for handicaps of quality or need, correspondingly. In contrast, reliability by design is independently of any evolutionary equilibrium state.

Signals that advertise the same Q_s compete with each other (Johnstone & Grafen, 1993; Møller & Pomiankowski, 1993; Iwasa & Pomiankowski, 1994). For all signal types except signals of need, efficiency increases as general costs decrease to minimum (Table 3). For all signals except handicaps and bluffs, the same is also true for Q_s . This leads signals to specialize, by their design, on qualities sought by recipients (either to handicap them or to expose or hide them). Signal specialization provides opportunities for co-existence of signals if selectors seek information about several different qualities or when signals use different reliability channels (for example, amplifiers can improve the perception of handicaps and co-exist with them; Hasson, 1990). This is where solutions may be found to questions a behavioral ecologist should ask, such as “how similar can signals be yet co-exist”, and “why are there so many kinds of signals?”

This study was partly supported by grants from the Schönbrunn and Vigivani Funds, and the United States–Israel Binational Science Foundation (BSF), Jerusalem, Israel. Burt Kotler commented on an early manuscript.

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