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Referential Signals

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I. ABSTRACT

Recent research on mechanisms of animal communication has been concerned largely with identifying the factors that have influenced the design of sexually-selected signals (II). Work in this area has produced exciting advances that integrate proximate and ultimate levels of analysis. It has, however, neglected a whole class of signals that encode information in addition to attributes of the sender. Birds and primates are now known to have specific calls that allow companions to predict environmental events, such as the discovery of food or the appearance of a particular type of predator (III). These signals are functionally referential.

I propose a framework for recognizing referential signals (IV), together with a strategy for the experimental analysis of such systems (V). Work on referential signalling is then reviewed, concentrating on the most obvious gaps in current models. I begin by considering the behaviour of callers, assessing production specificity (VI), the evidence for developmental plasticity in call usage (VIa) and some problems introduced by nomenclature (VIb). The factors responsible for transitions between different signal classes have been identified in some systems, but little is known about fine-grained variation in signal morphology. Conclusions about the information encoded in animal signals will be sensitive to the level of analysis selected because relatively gross changes, such as variation in call type, can reflect external events while more subtle variation in structure remains affective in nature (VII). The issue of signal design is then discussed. The factors responsible for determining the physical form of referential signals are much less well described than those that have shaped signals reflecting properties such as fighting ability or parasite load (VIII).

I suggest that there are aspects of signalling behaviour that cannot be understood by focussing only upon issues of meaning, but rather will require consideration of additional factors, including the likelihood of tonic communication and of signalling to predators. The contribution of contextual cues has probably been underestimated (IX). Social context plays an important role in determining whether signals are produced (IXa) and is thus an essential component in any model that seeks to predict calling behaviour. It is likely that contextual information also modulates the responses of receivers, both by providing additional information synchronous with the signal and by building up associations with particular signal types over the course of development (IXb).

I then assess critically some aspects of the relationship between communication and cognitive processes. Current evidence does not require us to conclude either that referential signals evoke representations of the eliciting event in the minds of receivers (X) or that they are used deceptively (XI). Finally, I consider the evolution of referential signals and suggest that ecological factors may have played an important role (XII).

II. MECHANISMS OF ANIMAL COMMUNICATION

The recent resurgence of interest in proximate questions concerning animal communication has been in large part driven by the realization that perceptual processes have influenced the design of animal signals (reviews by Guilford and Dawkins, 1991, 1993; Dawkins, 1993; Pagel, 1993; Guilford, 1995; Dawkins and Guilford, 1996). Although we have known for some time that the structure of songs and calls can be accounted for, at least in part, by considering the physical characteristics of the signalling environment (e.g., Wiley and Richards, 1982; Forest, 1994) it is only quite recently that we have begun to understand the role played by the properties of signal receivers. Analyses of sexually-dimorphic ‘advertisement’ signals, such as the conspicuous visual ornaments of birds, have been particularly revealing (e.g., M. Andersson, 1982, 1994; Møller, 1988, 1990; Barnard, 1990; S. Andersson, 1992). Such signals are likely to have arisen as a consequence of sexual selection operating through female mate choice, and this is thought to have affected not only the size of the structures, but also their degree of bilateral symmetry (e.g., Møller, 1992; Møller and Pomiankowski, 1993). In some cases, male signals appear to have evolved in response to pre-existing biases in female receivers. Systematic comparative analyses provide compelling support for the hypothesis that the evolution of the receiver preferences pre-dates those of the male traits (Basolo, 1990, 1995a,b; Ryan et al., 1990; Ryan and Rand, 1993). These examples illustrate the considerable benefits that may accrue from a research strategy that integrates analyses of proximate factors, traditionally the province of experimental psychology and neuroscience, with an exploration of the functional problems that have always assumed central importance in behavioural ecology. Such an approach is more likely to provide a comprehensive account of behaviour than a narrow focus on the issue of adaptive significance (Dawkins, 1989; Stamps 1991).

Theoretical models of animal communication increasingly stress the concept of ‘honest signalling’ (Zahavi, 1975). This view suggests that many animal calls and displays are costly to produce, and that they consequently provide reliable information about attributes such as resource holding potential (e.g., Clutton-Brock and Albon, 1979) or resistance to parasites (Hamilton and Zuk, 1982; Zuk et al., 1990a,b). Formal mathematical and neural net models have been developed to describe the evolution of handicaps and ornaments (Arak and Enquist, 1993; Johnstone, 1994).

III. REFERENTIAL SIGNALS

The theoretical and empirical advances described above have been almost exclusively concerned with displays that reflect the physical characteristics of the sender. This is not the only thing that animals signal about. Recent observational and experimental studies have demonstrated that some vocalizations encode not only individual attributes such as species, size, and motivational state, but also information about environmental events. Research on these systems, collectively termed ‘referential signals’, has been motivated by a very different set of theoretical concerns from those that provide the underpinning for studies of sexually-selected displays. The issues addressed have included the evolution of human language (e.g., Snowdon, 1993a; Evans and Marler, 1995) and the possibility that communication affords particular insights into the cognitive processes of non-human animals (e.g., Griffin, 1981, 1984, 1992; Cheney and Seyfarth, 1990, 1992). Analyses of referential signalling have proceeded along a parallel path, largely unaffected by recent developments in behavioural ecology. I suggest that this is unfortunate, both because studies of referential signals have not typically been concerned with issues of design, and because theoretical work on signal structure has largely ignored problems requiring an understanding of meaning.

I will not attempt a comprehensive summary of work on referential signalling, as this topic has been the subject of a number of recent reviews (Marler et al., 1992; Macedonia and Evans,

1993; Snowdon, 1993a,b; Evans and Marler, 1995; Hauser, 1996). Instead, I shall concentrate on what we do not know. My goal is not to denigrate the work that has so far been conducted, but rather to identify lacunae in our understanding of referential signals, in the hope that this will encourage additional research.

Traditional models of animal communication suggest that signals principally encode motivational information (e.g., Rowell and Hinde, 1962; Bastian, 1965; Lancaster, 1965; Premack, 1975; Luria, 1982). This theoretical position implies that variation in the sender's internal state will be reflected by continuous gradation in the physical properties of the signal produced. Signals will be evoked under a very wide range of environmental circumstances and will consequently only be interpretable with the aid of contextual information.

There are now several examples of call systems with quite different properties. Vervet monkeys (Struhsaker, 1967), ring-tailed lemurs (Macedonia, 1990), and chickens (Gyger et al., 1987), all have structurally-distinct alarm calls that are predator-class specific. Playback presentations of these alarm calls evoke adaptive responses from conspecific receivers (Seyfarth et al., 1980a,b; Macedonia, 1990; Evans et al., 1993a). These findings are consistent with the idea that the calls encode relatively specific information about the eliciting event (i.e., that they have the property of external reference) and are plainly incompatible with models relying on variation in motivational state, at least if this is conceived of in terms of general arousal.

It might, however, be possible to modify a motivational model to accommodate the specific eliciting conditions identified for the alarm calls of some primates and birds. This would be a challenging endeavour, because motivational accounts will have to explain the finding that call type is relatively insensitive to variation in the immediacy of threat posed by a predator. Vervets produce 'eagle alarms' to raptors, both when they are almost invisible in the distance, and when they are in the last phases of attack (Cheney and Seyfarth, 1990). Similarly, lemurs respond to avian predators with aerial alarm calls, and to carnivores with ground alarm calls, despite considerable variation, both natural and experimentally-simulated, in the danger posed (Pereira and Macedonia, 1991). Call usage in chickens also appears to be dependent upon the physical properties of predator stimuli, rather than upon apparent distance (Evans et al., 1993b). For a motivational model to accommodate these results, it is necessary to allow a proliferation of stimulus-type-specific affective states - so that, for example, vervets would be held to have three qualitatively distinct fear responses (corresponding to leopards, eagles, and snakes, respectively), that are evoked despite considerable variation in general arousal and subsequent behaviour. The existence of human phobias (Myers et al., 1984) demonstrates that such highly-specific fear responses are not inconceivable. It seems more parsimonious to suggest that vervet calls encode information about predator type than to rely on a complex model in which predators evoke discrete motivational states, which then evoke corresponding calls, but it is hard to imagine an empirical test that would distinguish between these alternatives.

A rather different theoretical position considers all of the information that is encoded in an animal signal. Smith (1981,1991, p. 214) suggests a relatively broad definition of the term 'referent' including "(a) several kinds of behavior (plus their probabilities and other variables), (b) physical characteristics of the signaller (e.g., its species and other identities), and (c) for some signals, external stimuli to which the signaller is responding." The more restrictive definition favoured by some authors, which focuses especially on the possibility of external referents (e.g., Seyfarth et al. 1980b; Marler 1985; Marler et al. 1992), approximates Smith's third category. It is important to note that if a class of signals were to encode highly-specific information about the sender's subsequent behaviour (category [a]), and if playback presentations were sufficient to elicit corresponding behaviour in respondents, then it would be

difficult to distinguish such signals from those that had external referents (category [c]). I suggest, however, that it is not necessary to treat behavioural referents and external referents as mutually exclusive interpretations. Vocalizations such as alarm calls make available many types of information about the sender; a partial list might include caller size, individual identity and affective state. It seems probable that such signals allow conspecific receivers some success in predicting the subsequent behaviour of the sender. This is perhaps especially likely to be true in species that have stable social groups with individually-distinctive vocalizations.

There are a number of other complications. For example, it is particularly difficult to determine whether signals should be thought of as denotative (i.e., as labels for stimulus categories) or imperative (i.e., as instructions describing appropriate responses) (Cheney and Seyfarth, 1990, 1992; Baron-Cohen, 1992; Marler et al., 1992). Attempts to explore the ‘meaning’ of animal signals also tempt us to address difficult philosophical issues, such as the level of intentionality required to explain the observed behaviour (e.g., Dennett, 1983; Cheney and Seyfarth, 1990) and whether animals are aware of their own knowledge or that of their companions (Allen, 1992; Armstrong, 1992; Schull and Smith, 1992; Snowdon, 1992). Problems of this kind are not unique to the study of animal communication; they are also characteristic of work on the behaviour of preverbal human infants (Marler et al., 1992).

I shall focus instead on questions that are clearly accessible to experimental investigation. Systematic studies of animal signal systems can only establish that our subjects behave *as if* their vocalizations encode information about events in the external environment. The term ‘functional reference’ has been coined to describe this property. It acknowledges the constraints inherent in analyses of animal signals, including the difficult distinctions described above (Marler et al., 1992), and is intended to be neutral about philosophical issues that are not addressed directly by empirical evidence.

IV. RECOGNIZING FUNCTIONAL REFERENCE

The discovery of referential signals in the natural behaviour of nonhuman primates and birds invites comparative and developmental studies. An essential prerequisite for such a program is the development of agreed criteria for recognizing the property of functional reference. Recent theoretical papers have suggested that this should involve consideration both of the caller’s behaviour and of the effects of the signal on companions (Marler et al., 1992; Macedonia and Evans, 1993). Studies of signal production and perception thus assume equal importance.

The key considerations with regard to production are that referential signals should be structurally discrete and that they should have a degree of stimulus-specificity. Eliciting stimuli should belong to a coherent category, although the absolute size of this category, and hence the degree of referential specificity, could vary considerably. Variation of this sort is also characteristic of human speech, which provides paradigmatic examples of referential signalling. We are able to denote individuals and also to discuss much larger groups that are delineated by characteristics such as age or occupation. Despite differences in the number of possible eliciting stimuli, the terms ‘Mary’ and ‘university professor’ are both unambiguously referential. The key point is thus not the absolute level of specificity, but rather the relationship between event class and signal type. We would not expect the same class of referential signal to be produced in response to stimuli that are clearly drawn from qualitatively distinct categories.

The importance of this distinction is illustrated by work on California ground squirrels. These sciurid rodents have a complex series of alarm calls which form a continuum from broad-band ‘chatters’ to tonal ‘whistles’ (Owings and Virginia, 1978). Whistles are usually produced in response to raptors, whereas chatter calls are evoked by terrestrial carnivores. However, there

are exceptions to this pattern of usage which suggest that the ground squirrel call system does not denote predator type. Squirrels being closely pursued by carnivores sometimes produce whistles, and chatters are given to distant hawks (Owings and Virginia, 1978; Leger et al., 1980; Owings and Leger, 1980). Similar patterns of call usage have been described in Belding's ground squirrels (Robinson, 1980, 1981; Sherman, 1985) and marmots (Blumstein, 1995a,b; Blumstein and Arnold, 1995; Blumstein, in press). The data on alarm call production in sciurids are consistent with the idea that these signals do not describe predator classes directly, but rather encode differences in response urgency perceived by the caller. This will vary quite reliably with predator type, as fast-moving hawks usually afford less time for escape than the relatively slow approach of a carnivore. Ground squirrels and marmots thus have call systems that are exquisitely well-matched to the hunting tactics of their two principal classes of predator; the signals are designed to allow receivers to judge the time available for fleeing to a burrow refuge, which is arguably information of greater functional importance than a taxonomic description of the approaching threat.

Signals with the property of functional reference must also meet a perception criterion. They should be sufficient, in the absence of the eliciting stimulus and of other normally available cues, to permit receivers to select appropriate responses. This property has been termed 'context independence' (Evans et al., 1993a; Macedonia and Evans, 1993). The most common technique for assessing perception of putative referential signals is playback experiments, in which recorded sounds are presented to conspecific receivers (e.g., Seyfarth et al., 1980b; Macedonia, 1990; Evans et al., 1993a). This approach, by design, strips away the contextual cues that might normally be provided by the non-vocal behaviour of the sender. Appropriate responses reveal that such information is not essential, but they do not demonstrate that it is unimportant (see below).

Theoretical papers discussing the issue of external reference in animal signals have traditionally employed a simple dichotomous classification scheme in which signals are considered to be either affective or referential (Marler, 1977, 1978, 1984; Gouzoules et al., 1985). More recent work has modelled the properties of animal signals as points falling along a continuum, with signals that principally reflect the motivational state of the sender, such as the distress calls of precocial birds (Collias and Joos, 1953; Abraham, 1974) and the cries of human infants (Lester, 1985), at one end, and affect-free referential signals, such as machine-generated speech, at the other. Categorizing a signal as functionally referential is equivalent to postulating a threshold value on such an underlying continuum, and then demonstrating empirically that the properties of the signal are such that it is exceeded. There is a degree of unavoidable arbitrariness inherent in partitioning any sort of variation in this fashion. It is also true that whether or not a signal meets the criteria described above will be dependent not only upon the characteristics of the system being studied, but also upon extraneous factors such as the number of animals available for study (and hence the level of statistical power), and the sensitivity of the response assays employed. The advantage of this approach is that it allows us to address issues, such as the development and phylogenetic distribution of referential signals, that would otherwise be intractable.

V. A STRATEGY FOR EXPERIMENTAL ANALYSIS

It is important to note that no single observation or experimental test is sufficient to identify the property of functional reference. Instead, we require a program of research that involves studies of both production and perception (Fig. 1). It is consequently not straightforward to obtain compelling evidence for referential signalling and this, combined with the very small number of systems that have so far been studied, suggests that we may have underestimated the incidence of this phenomenon.

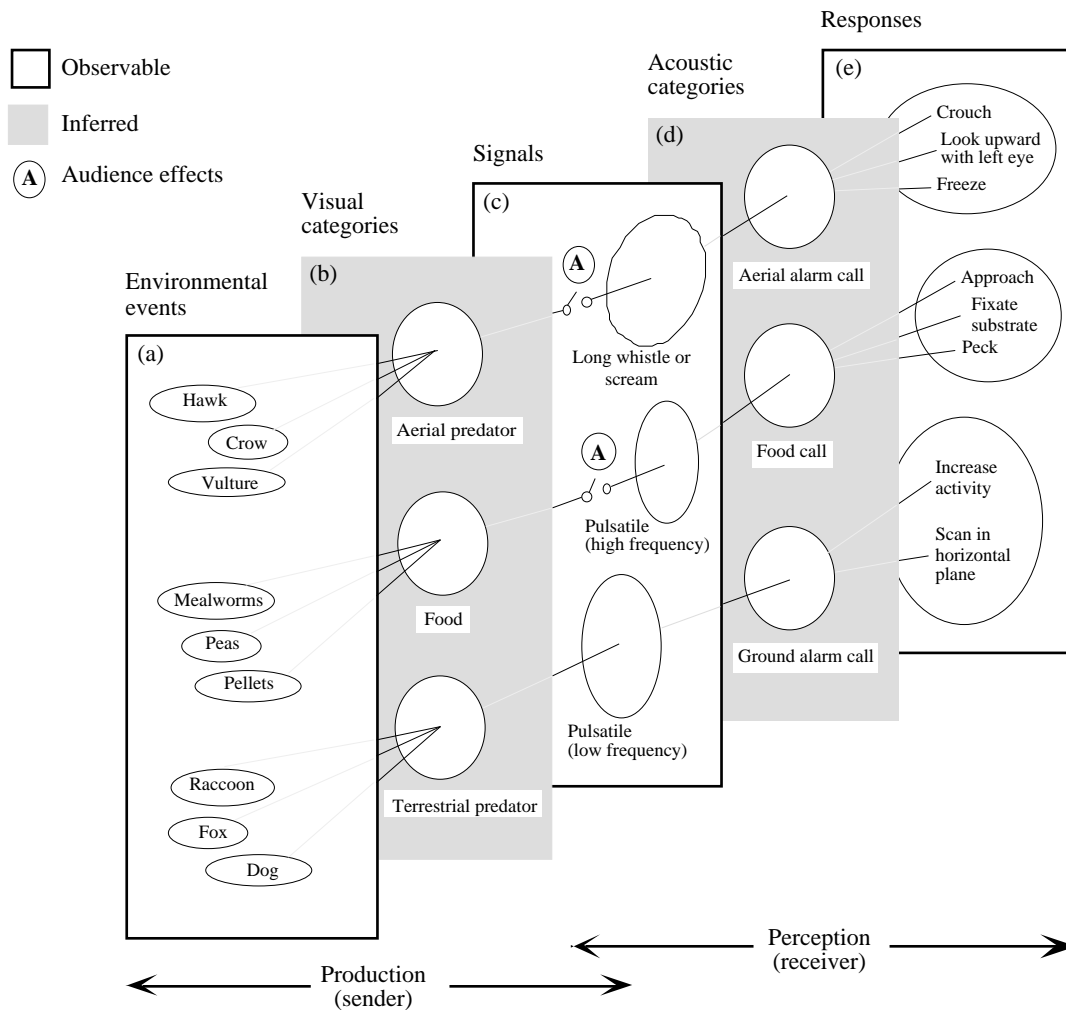


Figure 1: Functional reference in vocal signals. Examples summarize findings obtained from experimental analyses of the production and perception of chicken calls. The system has both observable and inferred properties (see text for details).

The strategy that I have outlined for exploring the properties of a system of putative referential signals involves mapping systematically the relationship between eliciting events (Fig. 1a) and signal morphology (Fig. 1c), and then assessing the effects of variation in signal-type (Fig. 1c) on receiver response (Fig. 1e). In addition to these three observable levels (stimulus characteristics, signal structure, and receiver response), I have included two hypothetical levels that are necessarily hidden and have properties that can only be inferred. I am assuming for heuristic purposes that visual stimuli do not evoke call production directly, but rather that they are first recognized as members of a category (Fig. 1b) which is then linked to a particular call type. There is some evidence for this idea, as call production is not obligatory on presentation of stimuli (see below). I have also included an analogous level in which categorization of call type by receivers occurs (Fig. 1d). There is evidence for such processing in both birds (Nelson and Marler, 1989; Dooling et al., 1990) and mammals (May et al., 1989; but see Ehret, 1992; Hopp et al., 1992).

This scheme for exploring the properties of referential signals can be illustrated by recent work on the vocal behaviour of chickens. Like all gallinaceous birds, chickens have a large vocal repertoire (Collias, 1987) which includes calls produced by both males and females upon discovering food and two structurally-distinct alarm calls, one associated with the approach of aerial predators and the other with terrestrial predators (Konishi, 1963; Collias, 1987). Initial

observational studies of the vocal behaviour of chickens under naturalistic conditions confirmed earlier descriptions of alarm call usage (e.g., Schjelderup-Ebbe, 1922; Collias and Joos, 1953; Baeumer, 1962; Konishi, 1963). Aerial alarm calls were evoked by a relatively broad class of objects moving overhead, while ground alarm calls were evoked primarily by stimuli such as humans and dogs (Gyger et al., 1987).

The structure of the two alarm call types is qualitatively distinct and can perhaps be regarded as antithetical. Aerial alarm calls are made up of an initial pulse, followed by a second component of much greater duration which can be either broad-band (scream-like) or narrow-band (whistle-like). Ground alarm calls, in contrast, are short, broad-band pulses, typically delivered in long bouts (Fig. 4 in Evans et al., 1993a). Studies of chicken alarm calling thus suggested that these signals might satisfy the production criterion for functional reference. They were evoked by coherent and non-overlapping sets of visual stimuli (Fig. 1a) and had discrete acoustic structure (Fig. 1c).

Subsequent laboratory experiments used videorecorded and computer-generated images of predators to confirm the relationship between predator class and the type of alarm call elicited (Evans et al., 1993a). The link between call type and receiver response was then assessed in a playback experiment. Upon hearing ground alarm calls, hens assumed an unusually erect, 'alert' posture and began scanning back and forth in the horizontal plane. In contrast, playback of aerial alarm calls evoked running toward cover, crouching with the feathers sleeked, and looking upward with one eye (Evans et al., 1993a). The hens thus behaved as though the call type predicted something about the circumstances under which the sound had originally been recorded. The responses evoked were precisely those that would facilitate detection of ground predators on the one hand, and of aerial predators on the other.

A peculiarity of the chicken visual system suggests that the type of information encoded, at least in aerial alarm calls, may be quite specific. There is a degree of hemispheric lateralization in the processing of visual stimuli such that the 'left eye system' and the 'right eye system' have different and complementary capabilities. The left eye system is superior for tasks involving spatial location, while the right eye system is better at some categorization tasks, such as the recognition of food (Andrew, 1988; Rashid and Andrew, 1989; Workman and Andrew, 1989). Following playback of aerial alarm calls, hens were much more likely to fixate upward with their left eye (Evans et al., 1993a). By doing so, they were bringing to bear the system best suited for locating a small rapidly-moving target such as an aerial predator. The pattern of results from studies of both production and perception is hence consistent with the idea that chicken alarm calls are functionally referential.

Male chickens produce distinctive 'food calls', both when they discover food during natural foraging behaviour (Gyger and Marler, 1988) and when they are provided with edible objects under controlled laboratory conditions (Marler et al., 1986a,b; Evans and Marler, 1994). Recent experiments using instrumental conditioning techniques to control access to food demonstrate that calling can also be evoked by an artificial stimulus (a red light) that reliably predicts feeding opportunities (Evans and Marler, 1994), suggesting that associative learning may be important in determining the range of events responded to (see below). The duration of food calls, like that of ground alarm calls, is brief, but food calls are easy to identify because they have distinctive frequency modulation and a reliably higher dominant frequency than ground alarm calls (Fig. 2 in Evans and Marler, 1994). Food calls thus appear to meet the production criterion of functional reference, although there are reports of 'deceptive' calling in the absence of food (Marler et al., 1986b; Gyger and Marler, 1988) that will require further investigation. I shall discuss the issue of deception in more detail below.

Published accounts of food call production do not, however, compel an interpretation of functional reference because they do not include complementary analyses of perception. Hens

respond to food calls by rapidly approaching the male, but we cannot exclude the possibility that this response is mediated by other aspects of the male's behaviour, such as visual displays, or by motivational factors quite unrelated to food, such as sexual receptivity. Interpretation of the data currently available on food-associated calls in chimpanzees (Hauser and Wrangham, 1987; Hauser et al., 1993; but see Clark and Wrangham, 1993,1994), golden lion tamarins (Benz et al., 1992; Benz 1993), toque macaques (Dittus, 1984) and rhesus macaques (Hauser and Marler 1993a) is similarly constrained by the lack of playback experiments. The idea of functional reference has the merit of making a clear theoretical prediction about the behaviour of hens, which is that presentation of food calls in the absence of other cues will be sufficient to elicit anticipatory feeding movements. Recently-completed experiments have confirmed this prediction. Hens approach a loudspeaker playing food calls, moving their heads repeatedly downward to fixate frontally on the substrate and occasionally pecking at the floor. These responses are significantly more probable during playback of food calls than during playback of either ground alarm calls (which are structurally-similar) or contact calls (which are produced under similar social circumstances) (Evans, in prep). The data from studies of production and perception thus suggest that chickens have a total of at least three functionally referential calls, which encode information about the discovery of food and about the appearance of predators (Fig. 1).

VI. SPECIFICITY

Analyses of referential signalling have always been concerned with the issue of specificity, that is, with the size of the stimulus set (Fig. 1a) corresponding to a particular call type (Fig. 1c). Analogies between the natural communication of animals and properties of human language (e.g., Cheney and Seyfarth, 1990; Evans and Marler, 1995) will be most compelling when animal signals are shown to be evoked by a small class of environmental events.

Unfortunately, we have data on so few referential systems that it is not yet possible to evaluate sensibly patterns of specificity. It is, however, clear that in some species the external stimuli evoking calls are quite narrowly-defined. For example, the 'eagle alarms' produced by adult vervet monkeys are elicited principally by martial eagles (Seyfarth and Cheney, 1980).

Comparisons between the morphology of martial eagles and those of the other raptors to which vervets give eagle alarms suggest that the monkeys may be responding not only to the overall form of potential predators, but also to quite subtle details, such as melanic markings beneath the head and under the wings, and perhaps also to dynamic cues such as characteristic differences in flight pattern.

Studies of the natural vocal behaviour of chickens provide a clear contrast to the vervet system. Chicken aerial alarm calls are associated with a relatively large set of airborne objects (Gyger et al., 1987). Laboratory experiments, in which birds were presented with computer-generated animations, have permitted the systematic manipulation of stimulus characteristics. The results demonstrate that aerial alarm calls are dependent upon attributes such as size and apparent speed (Evans et al., 1993b). Spatial location and shape are also important (Evans and Marler, in prep). These studies have provided a precise mapping of the stimulus parameters corresponding to call production and, together with measurements of non-vocal behaviour, they allow us to infer something about the way in which visual stimuli are recognized and categorized (Fig. 1b). Work of this kind is thus logically complementary to studies of visual categorization in animals using instrumental (e.g., Herrnstein et al., 1976; Herrnstein, 1984, 1991; Lea, 1984) or neurophysiological techniques (Kendrick and Baldwin, 1987; Perrett et al., 1987).

VIa. Developmental Plasticity

The specificity of calls produced by adult animals is likely to be a consequence not only of selection pressures operating over evolutionary time, but also of developmental factors.

Vervet infants clearly have a predisposition to respond to aerial objects with eagle alarm calls, but they initially respond to a much more diverse array of events than adults, so that their calls are associated not only with the appearance of potential predators, but also with innocuous birds such as storks and even with inanimate objects such as falling leaves (Cheney and Seyfarth, 1980). There is a marked increase in specificity over the course of development, and it may be relevant that the calls produced by juveniles in response to genuine predators are much more likely to be followed by adult calls than are their responses to non-threatening events. Observational data of this kind cannot, however, separate the effects of such experience from those of simple maturation.

Recent experimental studies of the development of alarm calling in chickens provide clear evidence for an effect of early experience (Palleroni and Marler, in prep). Chicks were reared under four experimental conditions. The first group was housed in an aviary together with the maternal hen and adult males. They received controlled exposure to a representative aerial predator (a trained falcon) and to a terrestrial predator (a ferret). The chicks were thus able to experience not only the morphology and distinctive hunting tactics of these two classes of predator, but also the calling behaviour and other responses of adult conspecifics. Three other groups were reared under conditions that lacked one or both of these types of experience. One group of chicks was exposed to predators but with no adults present, another group was reared with adult birds but had no experience of predators, and a third group was deprived of both types of experience. When they were six months old, the chicks from each of the four groups were presented with video-recorded sequences depicting both aerial and terrestrial predators. The chicks that had both predator experience and an opportunity to view the anti-predator behaviour of adults had normal responses, but the calling behaviour of each of the other three groups was deficient. These results suggest that development of fully competent adult anti-predator behaviour (i.e., responding to raptors with aerial alarm calls and to ferrets with ground alarm calls) is facilitated both by direct experience of the two predator classes and by exposure to the responses of adults.

Studies of development in both vervets and chickens hence provide evidence of developmental plasticity in the link between signal type and eliciting characteristics. There is, however, no suggestion of experiential effects on the physical characteristics of these signals. Vocal learning does not appear to occur either in the chicken (Konishi, 1963) or in nonhuman primates (Snowdon, 1990; Owren et al., 1992). These two model systems thus have only one of the two types of developmental plasticity characteristic of human language, in which both signal structure and the mapping between signal type and referent are dependent on the child's early environment (e.g., Locke, 1993). This is, nevertheless, a greater degree of malleability than might be expected in animal signalling systems, with the conspicuous exception of song development in oscine birds. It will be particularly interesting to determine whether the role of experience is to modify the relationship between eliciting stimuli and categorization (Fig. 1a-b), as is suggested by studies of predator recognition in other birds (Curio, 1993) and primates (Mineka, 1987; Mineka and Cook, 1987), or whether the link between category and signal type (Fig. 1b-c), may also be influenced.

VIb. Terminology

The problem of assessing referential specificity is complicated by issues of nomenclature. It is often necessary, for ease of exposition, to select labels for animal vocalizations that summarize the range of putative referents. The danger is that such terms bring with them a great deal of linguistic baggage and, perhaps unavoidably, a degree of ambiguity. For example, vervet 'leopard alarms' are also evoked by other animals, including eagles that are attacking (Cheney and Seyfarth, 1990) or feeding upon a dead vervet (Struhsaker, 1967), and pythons (M. Hauser, pers comm). They are also produced, although rarely, in the context of intergroup conflicts (Struhsaker, 1967; Cheney and Seyfarth, 1990). It is thus possible to

argue that the term ‘leopard alarm’ is misleading, because it connotes a greater degree of referential specificity than can be supported by the empirical data. Such criticism would, however, be unfair, because it is clear that the term ‘leopard’ was intended as a shorthand description for a category of eliciting stimuli of which large spotted cats are, if not the prototypical exemplar, at least the most common (Seyfarth et al., 1980b). Nevertheless, there is the real danger that the terms selected to describe eliciting conditions may reveal more about human linguistic conventions and about the categorization behaviour of the investigators than about the information content of the signals being studied. Such labels, when applied prematurely, may also affect the choice of future experiments (Snowdon, 1990). If a class of signals is labelled ‘food calls’ then we are perhaps less likely to conduct studies involving qualitatively different stimuli, even though they might reveal behaviour that would fundamentally alter our interpretation, such as calling during affiliative social interactions in the absence of food. Labels are rarely neutral; they reflect our intuition about the properties of the system being studied and they have the potential to constrain the direction of our research.

There are several possible solutions to the labelling problem. The first is suggested by the study of animal signals that do not have the property of functional reference. There is consequently no temptation to apply linguistic terms. The songs of birds or the calls of anuran amphibians are identified with labels that are either completely arbitrary or perhaps reflect some aspect of acoustic structure. This has, of course, been the traditional practice in studies of primate vocal behaviour, so that we read of ‘rough grunts’ in chimpanzees (Marler, 1976), ‘threat-alarm-barks’ in vervets (Struhsaker, 1967) and ‘isolation peeps’ in squirrel monkeys (Snowdon et al., 1985). It is difficult, however, to employ structural terms when faced with a vocal repertoire containing sounds for which we cannot readily coin onomatopoeic descriptions. The chicken’s vocal repertoire includes a number of pulsatile sounds that do not lend themselves to economical prose description, although the eliciting conditions (food, social affiliation, and approach of predators) do. One way to avoid this problem would be to use completely arbitrary terms that were neutral with regard to issues of call meaning - so that we might speak of pulsatile call1, pulsatile call2, and pulsatile call3. The obvious cost of such an approach is that our prose would become opaque and probably quite incomprehensible to the non-specialist. The demands of terminological precision are thus to some degree incompatible with those of eloquence.

The most straightforward solution might be to inform the reader at the outset about the way in which terms are to be used. We will then be able to discriminate between: (i) ‘leopard’ as a shorthand description for a category of calls with particular acoustic characteristics, elicited by, among other things, leopards, and (ii) ‘leopard’, a signal evoking mental representations of spotted cats in the minds of receivers, and sharing with some words the property of denoting a precisely-defined category of external objects. Clearly these two usages make very different claims about the cognitive underpinnings of the signal being studied, and they will be evaluated according to correspondingly different logical and empirical criteria.

VII. UNDERSTANDING VARIATION IN SIGNAL STRUCTURE: THE IMPORTANCE OF LEVELS

I have so far been discussing analyses that are concerned with variation at the level of call type. These involve identification of the eliciting event and of the factors mediating transitions from one signal class to another. Much less is known about the factors responsible for variation in signal structure within call type (Marler et al., 1992), although efforts have been made to ensure that such variation is represented in the exemplars chosen for use in playback experiments (e.g., Seyfarth et al., 1980b; Evans et al., 1993a). I suggest that the distinction between within-type and between-type variation is an important one, because systems may well prove to be referential at one level but not at the other.

Consider the properties of chicken food calls. These signals appear to be evoked by food items and by stimuli that reliably predict the availability of food. They are clearly not simply dependent upon social or sexual interaction (Evans and Marler, 1994). Analyses at the level of call type thus suggest that food calls predict events in the external environment (i.e., that they are functionally referential). There is also variation in the temporal characteristics of call bouts. The rate at which males produce food calls reflects their preference for a food stimulus, so that it is highest for live invertebrates and lower for less preferred items, such as their regular ration (Marler et al., 1986a). This relationship was initially considered to be evidence for highly-specific referential signalling about object characteristics (Marler et al., 1986a), but subsequent analyses have demonstrated that the call rate also co-varies with the speed at which males perform an operant task to obtain food. Males food called and key-pecked vigorously at the beginning of test sessions, but both of these responses decayed with repeated food deliveries (Evans and Marler, 1994). This correlation between instrumental performance and food calling suggests a more parsimonious explanation for the earlier results, which is that temporal variation may simply reflect the male's motivational state with regard to food. Analyses of food-associated calls in cotton-top tamarins suggest that this system may have similar properties. While 97% of tamarin calls were produced in the presence of food (Snowdon, 1993b), the rate of calling was dependent on idiosyncratic individual preferences for particular food types, and therefore most likely reflected a motivational response (Elowson et al., 1991).

Determining whether food-associated calls are functionally referential proves to be more complicated than we might at first suppose. I suggest that the answer obtained will be, in part, dependent upon the level of analysis selected. It is possible for transitions between call types to encode stimulus class while within-category variation in signal structure remains principally dependent upon motivational state. There is thus the very real danger that results from studies of fine-grained variation will appear to contradict those obtained from analyses of differences between call types when, in fact, these two data sets are not comparable because they concern quite different phenomena.

The challenge for future studies of fine-grained variation in referential signals will be to determine whether there are structural parameters that vary with stimulus characteristics, yet are independent of those that serve as vehicles for affect (Marler et al., 1992). Addressing this issue will require the systematic exploration both of the consequences of manipulating stimulus attributes and of variation in the internal state of the sender. Such experiments would begin to redress the relative neglect of motivational or 'conotative' factors in studies of referential signalling (Owings, 1994).

VIII. DESIGN OF REFERENTIAL SIGNALS

Analyses of the information content of referential signals have revealed that some systems have a surprising degree of specificity. This finding does much to explain both the calling behaviour of senders and the responses of receivers. Such work does not yet, however, allow us to make predictions about signal design. Clearly, we would expect calls that encode information about very different classes of events to have contrasting structure, and this is often true. But analyses of meaning provide little else in the way of insights into the physical form of referential signals. Why, for example, are vervet leopard alarms made up of a rapidly-repeated series of pulses with a relatively low fundamental frequency, while snake alarms are delivered at a lower rate and have a much higher dominant frequency, sometimes exceeding 16 kHz (Seyfarth et al., 1980b)? No-one has yet attempted a comprehensive model of the relationship between stimulus category and signal structure along the lines of Morton's (1977) motivational-structural rules, and given how little we still know about the details of referential signalling, such an effort would almost certainly be premature.

I suggest that a full account of any system of referential signals will need to consider issues in addition to that of call meaning, which has been the principal focus of most research conducted to date. Attempts to understand the information content of calls have necessarily been concerned with the correspondence between signal type and conditions of production, but there are a number of aspects of signalling behaviour that are not captured by such analyses. This point can be illustrated by comparing the properties of two alarm call systems in the chicken (Table I).

Table I: A comparison of alarm call design

Property	Aerial alarm calls	Ground alarm calls
Structure	Pulse + second component (wide or narrow band)	Repeated broad-band pulses
Amplitude	Low (after initial pulse) Very low after first call	Consistently high
Active space (detectability)	Small (especially second and subsequent calls)	Large
Localizability	Poor (especially second and subsequent calls)	Excellent
Audience effect	Yes	No
Duration of calling	Brief	Prolonged
Potential receivers	Nearby social companions	Conspecifics over large area + potential predator

Aerial alarm calls and ground alarm calls differ qualitatively in structure. Aerial alarm calls are low-amplitude vocalizations consisting of an initial pulse followed by a relatively long second component. Ground alarm calls are high-amplitude short pulses given in long bouts with an occasional 'scream' element. These characteristic differences in signal amplitude, which can exceed two orders of magnitude (Evans, unpub data), suggest that there will be reliable differences in the active space of the signals, with aerial alarm calls audible over a relatively small area, and ground alarm calls audible over a much larger one. This difference is particularly pronounced when we examine the structure of aerial alarm calls given after the initial response to a predator. These sounds are almost invariably narrow-band (whistle-like), typically lack the introductory pulse that may facilitate localization of the caller by conspecifics, and are so soft as to be almost inaudible. Ground alarm calls, in contrast, have acoustic characteristics, including rapid amplitude rise-time and broad frequency bandwidth, that should facilitate localization of the sender (Marler, 1955).

These differences in call structure are mirrored by differences in the duration of calling, and in non-vocal behaviour. Aerial alarm calls are typically given on first sighting a predator and are accompanied by 'crouching' and 'freezing' with prolonged immobility (Table I). Ground alarm calls have a very different time-course: call rate builds up quite gradually after spotting

the predator and calling may continue for some tens of seconds or even minutes after the predator has disappeared (Fig. 2 in Evans et al., 1993a). Long bouts of ground alarm calling are associated with increased motor activity, with the bird typically walking up and down vigorously in an erect posture (Table I).

In summary, both acoustic structure and the time-course of signalling suggest that aerial alarm calls are designed to allow the sender to remain cryptic, while ground alarm calls likely make the sender more conspicuous (Evans et al., 1993a). There are also reliable differences in the effects of an audience on these two call types. Aerial alarm calling is potentiated by the presence of conspecifics, regardless of age and sex (Karakashian et al., 1988), but there is no such audience effect on the production of ground alarm calls (Table I). Isolated males confronted with a terrestrial predator call at a rate indistinguishable from that of males with social companions (Evans and Marler, in prep).

It seems unlikely that considerations of call meaning will be sufficient to explain the signal characteristics and other behaviour summarized above. Certainly the continued production of ground alarm calls, long after a predator stimulus had disappeared, grossly exceeds the level of signalling required to warn social companions. This may be an example of tonic communication (Schleidt, 1973; Owings et al., 1986), in which signals function to maintain a state of vigilance appropriate to a predator that, although no longer visible, may still be nearby - as is typically the case with slow-moving carnivores. It is also possible that the overall pattern of results, incorporating differences in signal structure, time-course, and sensitivity to social context, reflects signalling to different potential receivers. Aerial alarm calls are ideally structured to alert flock members foraging nearby. The structure of ground alarm calls and the duration of calling are both consistent with the idea that although these signals are clearly salient to companions, they may also be designed to deter potential predators (e.g., Klump and Shalter, 1984; Caro, 1986a,b; Hasson, 1991; Caro et al., 1995). Assessing this idea will require quantitative estimates of the active space and localizability of alarm calls, not only for conspecifics but also for representative predators (e.g., Klump and Shalter, 1984). Observational studies of wild or feral populations will be necessary to determine whether animals engaging in ground alarm calling and associated conspicuous movements are indeed less likely to be attacked. Work of this kind has the potential to explain aspects of referential signal design that have so far been neglected.

IX. THE ROLE OF CONTEXT

IXa. Signal Production: Audience Effects

Classical treatments of animal signalling behaviour tend to assume that call production is essentially reflexive (e.g., Lyons, 1972). That is, that when a sufficient stimulus (e.g., a predator model or a food item) is presented, then the appropriate call, together with other responses (anti-predator behaviour or feeding) will necessarily be evoked. Recent work on a taxonomically-diverse array of species demonstrates that such simple models are inadequate. Ground squirrels (Sherman, 1977; Owings et al., 1986), marmots (Blumstein et al., in press), vervet monkeys (Cheney and Seyfarth, 1985), downy woodpeckers (Sullivan, 1985), and chickens (Marler et al., 1986b; Karakashian et al., 1988; Evans and Marler, 1991, 1992, 1994) all modulate their vocal behaviour according to social context.

In some systems at least, these 'audience effects' appear to be specific to vocal behaviour. Chickens respond with anti-predator behaviour when presented with simple, hawk-shaped models of the kind used in the classic experiments of Lorenz and Tinbergen (Tinbergen, 1948), or computer-generated animations of aerial predators (Evans and Marler, 1992; Evans et al., 1993a,b), and this has allowed exploration of the effects of social context under controlled conditions. Alarm calls are produced by cocks when there are conspecifics present, but not

when they are alone (Karakashian et al., 1988; Evans and Marler, 1991). Comparisons of the non-vocal responses to simulated predators reveal no apparent differences. Behaviour such as crouching down, sleeking the feathers and fixating on the stimulus appears to be insensitive to social context, while call production is profoundly affected (Karakashian et al., 1988; Evans and Marler, 1991, 1992).

Studies of food calling provide opportunities for particularly sensitive comparisons between the effects of an audience on signalling and those on non-vocal behaviour because animals will readily perform instrumental tasks to obtain food. If the food-delivery apparatus is computer-controlled, then it is possible to evaluate, moment-by-moment, the rate at which the subject works, perform synchronous analyses of signal structure, and then assess changes in both of these measures as a function of social context. This approach has recently been employed to explore the audience effect on food calling in chickens (Evans and Marler, 1994). Cocks were trained to peck a key for food reinforcement and then tested both in social isolation and with a female audience. Males produced significantly more food calls when a hen was confined in an adjacent cage than when they were alone, but the rate at which they keypecked was unaffected (Evans and Marler, 1994). At least under the conditions of this experiment, the presence of an audience potentiated calling in a specific fashion. It is therefore possible to reject the suggestion that the audience effect is simply a manifestation of social facilitation (Dewsbury, 1992), as this would be expected to affect both call production and feeding behaviour (e.g., Zajonc, 1965).

The discovery of audience effects implies that any model seeking to predict the signalling behaviour of animals will require consideration not only of the obvious environmental events, but also of social context. The presence of companions can be conceived of as modulating, either attenuating or enhancing, the link between stimulus categorization and vocal response (Fig. 1b-c).

IXb. Signal Perception: Immediate And Historical Context

The finding that some animal vocalizations appear to encode specific information about environmental events has stimulated quite extensive work focussing on the information content of calls. It is perhaps inevitable that this has led to the relative neglect of contextual cues (Leger, 1993). Contextual factors are, however, likely to play an important role in the perception of signals (Fig. 1c-e) (Smith, 1965, 1977, 1991; Leger, 1993). Playback experiments, which assess the responses evoked by a call in the absence of cues that are normally provided by the non-vocal behaviour of the sender, strip away information that is potentially provided by 'immediate context' (Smith, 1991; Leger, 1993). If conspecifics are nevertheless able to select appropriate responses, then it follows that such cues are not essential, but this does not suggest that the animals being studied are insensitive to non-signalling behaviour when it can be monitored. Indeed, accounts of experiments in which referential calls have been presented to members of a social group typically describe behavioural responses, such as looking toward the loudspeaker (Seyfarth et al., 1980b), that are consistent with an attempt to evaluate the sender's non-vocal behaviour, and perhaps to learn more about the environmental situation in which the call was produced. The relatively loud and easily-locatable pulse element at the beginning of chicken alarm calls (Gyger et al., 1987) reliably evokes orienting responses from the other members of a group, and birds may well then be able to acquire much more specific information about eliciting conditions, because the caller is typically crouching and fixating upon the approaching predator (Evans, unpub data).

Experimental investigations of the role played by immediate context have also been constrained by the technical difficulty of manipulating non-vocal behaviour in a controlled way. The recent finding that a number of species respond socially to video-recorded images of conspecifics

(Clark and Uetz, 1990, 1991, 1993; Evans and Marler, 1991; McQuoid and Galef, 1993; Macedonia et al., 1994; Macedonia and Stamps, 1994; Rowland et al., 1995a,b; Rosenthal et al., 1996) suggests a strategy for overcoming this obstacle. It should be possible to conduct experiments in which both signal and non-signal behaviour are systematically varied, with the goal of identifying the way in which immediate context interacts with call morphology to determine receiver response.

Animals are also sensitive to 'historical' context (Smith, 1991), that is, to the prior relationships between signals and environmental events. This is suggested by responsiveness to factors such as variation in sender 'reliability' (i.e., the correlation between individually-distinctive calls and occurrence of a particular class of eliciting stimuli; Cheney and Seyfarth, 1988). The recent finding of developmental plasticity in the alarm calling behaviour of chickens exposed to different regimes of predator experience (Palleroni and Marler, in prep) similarly demonstrates an effect of historical event-signal relationships.

It might prove revealing to examine variation in the responsiveness of animals to functionally referential signals as a consequence of environmental cues. For example, do birds and primates become more sensitive to playback of alarm calls when they are in a part of their home range in which they have previously experienced attacks by the same class of predator that evoked the call? It is easy to imagine habitat features that predict a higher probability of attack by particular types of predator (e.g., areas of dense cover are more likely to conceal carnivores than open grassland). If associations of this type prove to be an important determinant of the level of responsiveness to alarm signals, then there will be implications for the interpretation of playback experiments. In field studies, it would be necessary to add controls for subject location at the moment of call presentation, or at least to systematically sample the responses evoked in different parts of a home range. In laboratory experiments, consideration will have to be given to the possibility that animals placed in a completely novel environment might have attenuated responses to conspecific signals, because the test situation provides none of the historical context cues that would normally facilitate selection of appropriate behaviour. It follows that such experiments may be particularly conservative tests for functional reference.

X. REPRESENTATIONS: ARE THEY IN OUR MINDS OR THE ANIMALS'?

Highly-specific animal signals appear to share with some words the property of identifying environmental events. This analogy might, however, be less exact than it at first appears. Words correspond to mental representations instead of denoting objects directly. The term 'functionally referential' explicitly acknowledges that, although animals behave as though their signals provide information about external stimuli, and although this is consistent with the responses being mediated by mental representations, it does not compel such an interpretation. One way to consider representations is as an intervening variable (e.g., Hinde, 1974) so that instead of signals eliciting behaviour directly (signal --> behaviour), there is an intervening layer (signal --> representation of eliciting conditions --> behaviour). We would be inclined to reject the latter account for reasons of parsimony unless there was some direct evidence for an intermediate level of processing.

Cheney and Seyfarth have conducted a series of field playback experiments designed expressly to determine whether the responses of vervet monkeys to conspecific alarm calls are mediated by mental representations (Cheney and Seyfarth, 1988). A subsequent experiment, which I will not discuss in detail, compared processing of vervet and superb starling alarm calls (Seyfarth and Cheney, 1990). Both studies employed a habituation/dishabituation paradigm that had previously been used in research on preverbal human infants: Vervets were first played a single exemplar of one call type (baseline). They then received a series of eight presentations of a different call (habituation) followed by a second presentation of the call heard

initially (test). The critical comparison was of the duration of responses following the initial baseline presentation with those evoked by the final test presentation.

The experiments exploring the vervets' responses to calls produced by their companions (Cheney and Seyfarth, 1988) involved systematic manipulations of the relationship between the baseline/test stimulus and the sounds used in the intervening habituation series, varying acoustic structure, individual identity of the caller, and the putative referent. There was a significant decrement in the response to a 'chutter' call (characteristic of intergroup interactions) when the baseline and test presentations were separated by an repeated presentations of the same individual's 'wrr' (another call type characteristic of interactions with neighboring groups). No such decrement was obtained when the habituation series was a 'wrr' recorded from another individual. Analogous experiments assessed response to leopard or eagle alarms, with a habituation series made up of the other type of alarm call recorded either from the same individual as the baseline/test stimulus, or from a different individual. There were no statistically significant differences between the responses to baseline and test presentations in these trials.

Cheney and Seyfarth suggest that the results from their habituation/dishabituation studies demonstrate that the principal determinant of the vervets' responses was the meaning of the calls presented, rather than their physical structure, and argue that this provides the strongest evidence available for *representational* signalling (Cheney and Seyfarth, 1988, 1990, 1992; Seyfarth and Cheney, 1992, 1993). Specifically, it is claimed that vervet monkeys, "appear to process information at a semantic level, and not just according to acoustic similarity" (Cheney and Seyfarth, 1988), and that "monkeys have some representation of the objects and events denoted by different call types and that they compare and respond to vocalizations on the basis of these representations" (Seyfarth and Cheney, 1993). If true, these claims represent an important advance in our understanding of the cognitive capabilities of non-human primates, extending substantially the parallels between referential signalling and human speech. The case for representations has additional theoretical importance because it is part of the foundation upon which subsequent arguments are constructed. These include consideration of more complex cognitive processes, such as the possibility that vervets attribute mental states (e.g., knowledge or belief) to their companions (Cheney and Seyfarth, 1990, 1992), and can thus be said to have a 'theory of mind'.

The conclusion that the responses of vervet monkeys to alarm calls are mediated by mental representations is based upon two assertions: (i) that the results obtained cannot be accounted for simply in terms of physical differences between the stimuli, as in traditional habituation/dishabituation studies (e.g., Nelson and Marler, 1989), and (ii) that differences in the duration of response between baseline and test presentations are attributable to the intervening habituation experience. I shall discuss each of these issues in turn.

Cheney and Seyfarth provide descriptive statistics for a selection of call characteristics such as total duration, dominant frequency, fundamental frequency, and voicing. They conclude that the structural properties of the intergroup calls (wrr and chutter) were not more similar than those of the leopard and eagle alarms, and suggest that the acoustic characteristics of the playback stimuli cannot therefore account for the results obtained (Cheney and Seyfarth, 1988). Quantitative analyses of this kind are an essential first step in exploring the recognition and categorization of animal signals, although the data provided are not sufficient to provide a comprehensive mapping of the acoustic space occupied by the calls in the vervet repertoire, as has been possible for analogous descriptions of other signals (e.g., Marler and Pickert, 1984; Nelson and Marler, 1990). A more serious concern, however, is that there is no way of assessing the perceptual significance of the acoustic features selected. Systematic playback experiments involving either titration along acoustic continua (e.g., Gerhardt, 1978; Zoloth et

al., 1979; Evans, 1993), or the use of a very large number of natural sounds together with multidimensional scaling analysis (e.g. Dooling et al. 1990) would be necessary to establish the way in which vervets partition the acoustic space occupied by their vocalizations. Ideally, perception of the calls would be analysed in sufficient detail that the ‘weighting’ assigned to each acoustic feature could be estimated (e.g., Becker, 1982; Gaioni and Evans, 1986; Nelson, 1988; Weary, 1990, 1991; Gerhardt, 1992). There would then be an empirical basis for comparing the differences (not physical, but perceived) between the pairs of sounds that produced significant decrements in habituation experiments and those that did not. In the absence of such analyses, there is no compelling reason to reject a traditional interpretation based purely upon the physical properties of the playback stimuli.

A separate concern about the habituation/dishabituation technique employed by Cheney and Seyfarth (1988) is that the design lacks essential controls. Recall that the experiments involved presenting one type of sound (a1), followed by repeated presentation of another sound (b1 - b8), and, finally, by a test presentation of the first sound heard (a2). Statistical comparisons were between the responses evoked by the initial and final presentations (i.e., a1 vs a2). A significant decrement in responding is described as “transfer of habituation” and is taken as evidence that the representations for sounds from classes ‘a’ and ‘b’ are similar. But this is the wrong logical comparison. What is required is an assessment of the response to a second presentation of sound ‘a’ when this has followed repeated playback of sound ‘b’ with the response to a second presentation of sound ‘a’ in the absence of such an intervening experience. This would require a parallel series of experiments in which some animals heard the sounds, as described by Cheney and Seyfarth, while a control group heard an initial playback of sound type ‘a’ (A1) followed, after the same period of elapsed time as in the habituation series, by a second presentation (A2):

Habituation	a1	b1 - b8	a2
Control	A1		A2

Comparisons between the responses evoked by a2 and A2 would, if significant, suggest that the intervening experience with ‘b’ had affected responsiveness. The comparisons reported are uninterpretable, because the possibility cannot be excluded that a second presentation of ‘a’ would have evoked a smaller response *regardless of the intervening experience*. Assuming that more straightforward explanations based solely upon the physical structure of the sounds could be ruled out, this modified design would have the potential to provide evidence for representational signalling.

Note that nothing in the preceding discussion demonstrates that vervet alarms do not evoke mental representations in the minds of their companions. It is entirely possible that they do. I suggest, however, that the results reported so far do not require us to make such an inference.

Xa. Some Alternative Approaches

Work on instrumental conditioning suggests a different strategy for assessing whether the effects of referential signals are dependent upon representations of the eliciting event. Experiments in which the ‘value’ of a reinforcer (food or sucrose liquid) was diminished, either by pairing it with a toxin or by satiation, demonstrate that these manipulations reduced the rate at which rats performed an instrumental response (bar-pressing or chain-pulling). It follows that the rats’ behaviour was influenced by a stored representation of reinforcer properties (Colwill and Rescorla, 1985).

Similar logic could be applied in experimental analyses of responses to referential signals. If calls evoke particular behavioural responses in an essentially reflexive fashion, then changing the animal’s experience with a class of visual stimuli (e.g., food or predators) should not alter

the effects of presenting recorded sounds. If, on the other hand, calls affect behaviour by representing a particular class of events, then increasing or decreasing the salience of these events should also perturb the response to the corresponding signals. For example, if chicken food calls cause hens to approach because they evoke a representation of palatable objects, then an experience that reduces the value of such objects should also attenuate responsiveness to the calls. This argument generates a strong prediction, which is that birds should approach a loudspeaker playing back food calls more rapidly when they are hungry than when they are satiated. The effects of manipulating hunger should also be specific to food calls, and should not affect responsiveness to other signals in the vocal repertoire.

Conceptually similar experiments could be conducted with alarm calls. It should be possible to increase or decrease the salience of simulated predators by using conditioned fear (e.g., Mineka, 1987; Mineka and Cook, 1987) and habituation paradigms. In systems where there is more than one type of alarm call, there is the opportunity to design a highly sensitive assay, because animals could be habituated to one set of putative referents (e.g., terrestrial predators) while leaving their experience of the other set (e.g., aerial predators) unaffected. The prediction in this case would be a selective reduction in responsiveness to ground alarm calls, with no change in responsiveness to aerial alarm calls. Control groups could be exposed to the opposite pattern of experiences (i.e., habituated to aerial predators). In both cases, presentations of alarm calls provide a particularly specific test, because it would be possible to discriminate a reduction in responsiveness to one class of predator from a more generalized diminution in fearfulness.

A recent report describing social interactions between junglefowl cocks and hens confined in a small arena suggests that manipulating hunger might not produce the predicted change in responsiveness to food calls (Van Kampen, 1994). Hens that had been food-deprived for 24 hours were no more likely to approach a male than when they had experienced *ad lib* access to food. This result is said to demonstrate that “hunger state is not a factor in determining the reaction of females to male food-calling”. Unfortunately, no quantitative analyses of male vocal behaviour are provided; it is consequently not feasible to verify that the sounds produced by cocks in Van Kampen’s (1994) experiments are comparable with those that have been the subject of other studies (e.g., Evans and Marler, 1994). It is also impossible to assess the effects of control sounds (none were presented), to compare female responses to calling males with those to silent males, or even to partition out the contribution of vocal signals relative to other male behaviour such as courtship displays. A similar manipulation of sexual motivation, which compared the behaviour of hens that had been isolated for six days with that of hens maintained in a social group with a male, also failed to reveal any differences in the probability of approach (Van Kampen, 1994). It is quite possible that the negative results obtained in both of these experiments are simply attributable to the small sample size employed. I suggest that the relationship between the responses evoked by food calls and the motivational state of receivers might repay further investigation.

Experiments like those outlined above have the potential to provide strong evidence that referential signals affect receiver behaviour by evoking representations. Note, however, that the results obtained would only establish the existence of ‘nominal representations’ (i.e., that the calls stand for something in the environment; Gallistel, 1990). This would be an important finding, but it should be noted that nominal representations are the most basic type; they are a relatively impoverished cognitive phenomenon compared with the ‘computational representations’ thought to be involved in processing information about time and spatial location (Gallistel, 1990). The use of the term ‘representational’ to describe the properties of animal signals certainly need not connote the sophistication implied by the linguistic use of the same term, in which representations have predicates (e.g., the brown dog that has fleas).

There are paradigms in which there is a consensus that representations are necessary constructs for explaining behaviour. One clear example is filial imprinting (e.g., Hollis et al., 1991; Johnson, 1992; Bateson and Horn, 1994). Here there is compelling evidence that chicks store information about the characteristics of the maternal hen, and the neurophysiological basis of this process is now understood in some detail (Horn, 1985; 1990; Honey et al., 1995). The considerable time-lag that may elapse between exposure to an imprinting object and successful performance on a discrimination task makes the inference that behaviour is dependent on a stored representation unavoidable. This work suggests another possible approach for evaluating whether or not functionally referential signals are also representational. Experiments could be designed to assess whether exposure to referential signals significantly affects subsequent behaviour measured hours or days later. For example, if birds were exposed to aerial alarm calls in one context, perhaps arranged to be visually distinctive, would they then be persistently more likely to engage in behaviour that functions to detect aerial predators (e.g., scanning upward) than in other environments of a similar type? This strategy for detecting representations relies upon tests to determine whether changes in behaviour caused by signals are based on memories stored for longer periods than the seconds or minutes that normally elapse in playback experiments. Intriguingly, there is anecdotal evidence to suggest that playback of snake alarms affected the behaviour of vervet monkeys passing through the same area some hours later (Cheney and Seyfarth, 1990) but systematic experimental tests would be required to verify this.

XI THE PROBLEM OF DECEPTIVE SIGNALLING

There is probably no single issue that has generated more philosophical interest and debate than the possibility that animals are capable of behaving deceptively (Griffin, 1981, 1984, 1992; Ristau, 1983; Mitchell and Thompson, 1986; Whiten and Byrne, 1988; Byrne and Whiten, 1990, 1991). This is perhaps because successful deception requires a degree of cognitive complexity and flexibility in behaviour that is qualitatively distinct from that envisaged both in traditional ethological accounts and in behaviourist analyses. As such, strong evidence for deception in the vernacular sense narrows considerably the gap between the cognitive properties of non-human animals and those that we impute to other humans. Like the issue of language, the problem of deception bears directly on the degree of continuity between humans and non-human animals and on the question of human uniqueness.

I will focus especially on deceptive signalling in the specific sense of transmitting false information about external events. I shall argue that analyses of referential signals make a critical contribution to understanding whether this phenomenon occurs in the natural behaviour of animals.

It is important to be rigorous in separating the cognitive use of 'deception' from a purely functional one (Mitchell, 1986). The Batesian mimicry of the viceroy butterfly provides a classic example of functional deception, but this hardly encourages us to speculate about its mental state. It is not, however, always straightforward to deduce which of these senses is intended in published accounts of deceptive behaviour (see below).

There are several types of evidence for deception in animals. The first relies on the systematic collection and analysis of unique social interactions. These anecdotes are then assembled and examined to determine whether there are consistent trends (e.g., Whiten and Byrne, 1988). The second involves studies of inter-specific communication, focussing upon signals that are designed to affect the behaviour of potential predators (e.g., Ristau, 1983, 1991). And the third, which I will concentrate on here, involves intra-specific communication and the selective production of signals that are normally evoked by the approach of predators or the discovery of food. It is logical to separate these latter two data sets because there are likely to be important

differences between inter- and intra-specific signals, both in the contingencies controlling production from moment-to-moment and in the selection pressures that have defined signal properties over evolutionary time. Evidence for deceptive intra-specific signals can be further sub-divided into instances of animals ‘withholding’ signals under conditions in which they are usually produced, and examples of signalling in the absence of the putative referent. I shall refer to the former as ‘passive deception’ and to the latter as ‘active deception’.

XIa. Passive Deception

It is often suggested that remaining silent under conditions where a signal would normally be given is likely to be the most common form of deception in animal communication because the odds of retribution from companions are low (e.g., Cheney and Seyfarth, 1990; Hauser, 1992; Hauser and Marler, 1993a,b). There are, however, serious difficulties in interpreting the absence of behaviour (Snowdon, 1992). It is always difficult to exclude the possibility that the normal eliciting conditions for the signal are not sufficiently well-understood and that some critical factor is simply absent on those occasions when signals are not evoked. In order to make a more compelling case for the inhibition of signalling, it would be necessary to demonstrate that the state of the sender when no signal is produced is otherwise identical with that when signals are given. This will require additional response assays, perhaps including physiological measures, and will be a methodologically-challenging enterprise. Even if such data were available, the inference of deception would still be vulnerable on logical grounds, because it would involve asserting the null hypothesis. It will always be possible to suggest (and this argument will have some force) that a failure to demonstrate differences in physiological state, or in other non-signalling responses to an eliciting event, is simply an artifact of assay insensitivity. I believe that it will consequently be difficult to make a truly compelling case for ‘passive deception’.

An additional complication is introduced if we consider the information content of a signal in a broader sense. For example, food calls are likely to encode information not only about the availability of food but also about the subsequent behaviour of the sender (Evans and Marler, 1994). Male chickens that food call at high rates typically refrain from ingesting the food item themselves and allow hens that approach to take it instead. The call thus predicts not only the presence of a palatable object but also a low probability of aggression by the sender. A striking contrast is apparent when this is compared with that of the behaviour of the same cock in the presence of a rival male. Under these conditions, call production is almost completely abolished (Marler et. al., 1986b). If our analyses were concerned solely with characteristics of the eliciting stimulus, then we might infer that this was a case of passive deception and that the silent males were concealing from competitors the presence of a valuable and limited resource. If however, we consider other information in the signal, so that the meaning is not simply “food” but “food + a preparedness to share it”, then there is no need to posit deception because the call is an honest commentary on the male’s likely subsequent behaviour (see Smith, 1991).

XIb. Active Deception

There is clearly the potential to construct a more logically-compelling case for deception in situations where signals are produced in the absence of the events that normally elicit them. In such instances, we are dealing with overt behaviour and are no longer handicapped by the requirement to demonstrate that a signal ‘should’ have been produced, as in the case of passive deception. However, it is often very difficult to determine whether a case is being made for deception in a cognitive sense, suggesting parallels with the most sophisticated aspects of human social behaviour, or whether the term is simply intended in a less controversial functional sense. I shall illustrate this distinction with an example based loosely on work by Munn (1986a,b) and by Møller (1988).

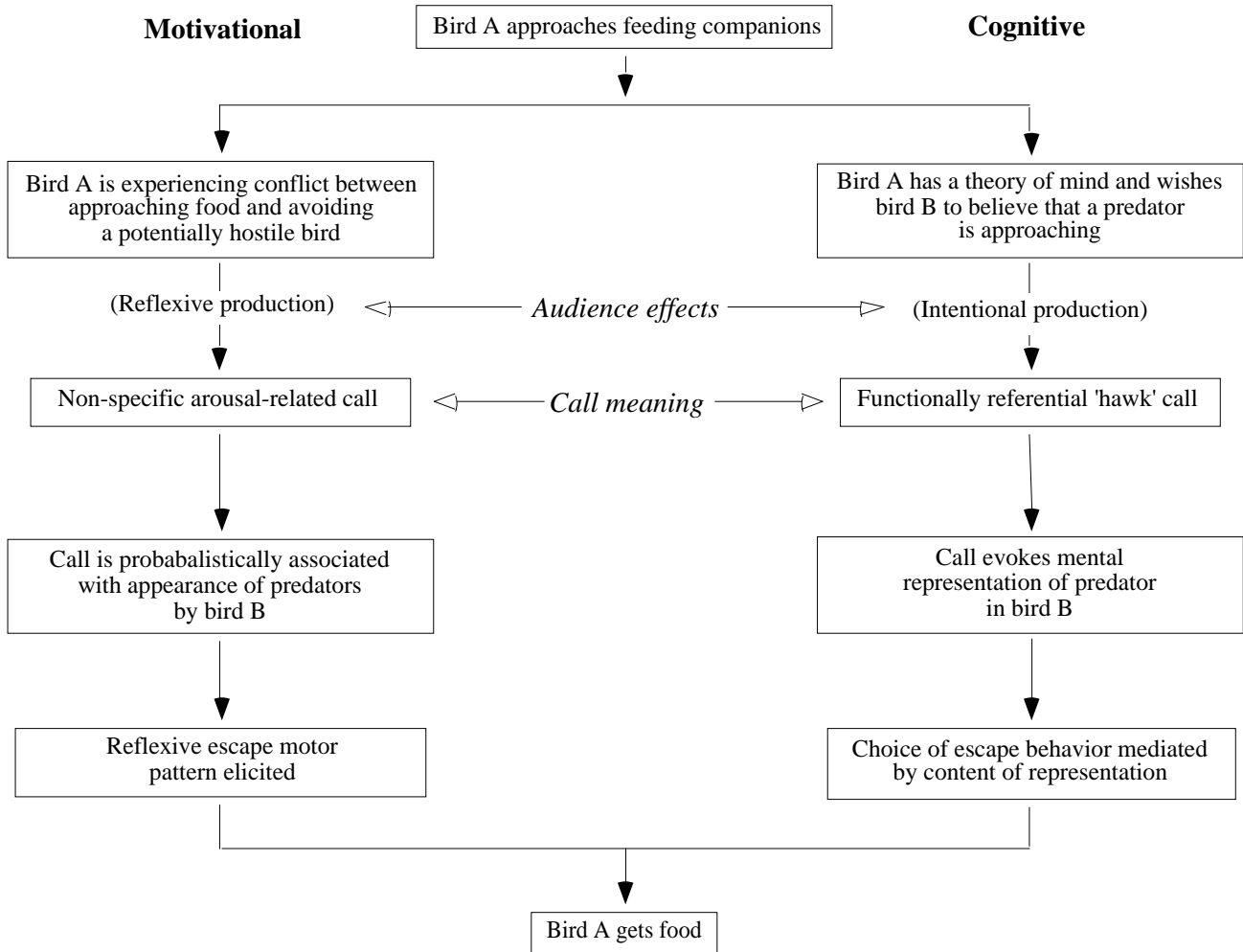


Figure 2: Two alternative explanations for an observation of ‘deceptive’ alarm calling. The motivational model depends upon reflexive responses (perhaps attributable to associative learning) and changes in arousal. The cognitive model postulates sophisticated mental processing by both sender and receiver. Discriminating between these mechanisms requires analyses of call meaning and audience effects.

Consider the problem of interpreting the following observation (Fig. 2). Bird A is approaching bird B, which is feeding on a rare and highly-preferred food item. Bird A suddenly produces an alarm call, normally associated with the appearance of a hunting raptor. Bird B responds by dropping the food item and flying into cover nearby. Bird A then picks up and ingests the food. This is clearly a case of deception in the functional sense: bird A has altered the behaviour of bird B in such a way that it benefits and bird B does not. There are parallels between such uses of vocal signals and traditional examples of deceptive signalling that involve morphological characters, as in the case of Batesian mimicry. This analogy raises a series of intriguing questions about the factors selecting for deceptive signals and for maintaining them in the population over evolutionary time (Guilford and Dawkins, 1991, 1993). It does not however, require us to infer that the alarm call is also deceptive in a cognitive sense. There are several possible proximate explanations for bird A’s behaviour. I have outlined two quite different accounts, deliberately selected so as to illustrate the contrast between them.

The first explanation, which draws on ideas from classical ethology, is principally concerned with motivational factors. Bird A approaches feeding companions and experiences an approach / avoidance conflict because it is attracted to the food but fearful of the potentially hostile individual currently in possession of it. The motivational conflict triggers a reflexive alarm call.

This vocalization is a non-specific signal reflecting bird A's internal state (i.e., high levels of arousal), which is usually associated with the appearance of predators. This contingency is responsible for the call evoking an escape response from bird B.

The alternative cognitive account could be outlined as follows: bird A has a theory of mind and wishes bird B to believe that a predator is approaching. To create this belief in bird B, bird A intentionally produces a highly-specific referential alarm call. This evokes a mental representation of an approaching predator in bird B, which, in turn, mediates the choice of escape behaviour. Bird B elects to flee to cover, which is the most appropriate response for avoiding an aerial predator.

Both of these models describe signalling that is deceptive in the functional sense, and if we were concerned solely with the fitness consequences of behaviour, we would have no need to choose between them. Only the cognitive account would constitute deceptive behaviour in the vernacular sense. Note that discriminating between these alternatives depends heavily upon understanding the type of information encoded in the signal. I do not believe that a convincing case can be made for deception in the cognitive sense if the signal does not meet the criteria for functional reference, because it would then be simply an accurate commentary on the internal state of the sender. Other components of the cognitive account may be less important and intermediate positions are surely possible. For example, we might choose to define cognitive deception in such a way that call production need not be intentional. A decision on this point will depend upon a more detailed understanding of the nature of audience effects and of whether or not they reflect volitional signalling. We may similarly be able to dispense with the requirement that birds have a 'theory of mind', or perhaps be able to take a neutral position on this issue, because it is likely to be intractable to experimental investigation.

The issue of call meaning, however, remains central. In many recent accounts of deceptive signalling, it is not clear whether the authors intend the functional or the cognitive sense, although reviews often assume the latter (e.g., Ristau, 1991; Griffin, 1992; Gould and Gould, 1994). There are typically not sufficient data to make a case for referential signalling, so the functional interpretation might be preferred on grounds of parsimony. For example, in Møller's analysis of alarm calling by great tits (Møller, 1988), and Munn's description of alarm calling in shrikes (Munn, 1986a,b), we do not have the necessary information about production and perception to establish call meaning. This is not a serious deficiency in either account, because the authors are principally concerned with the functional consequences of signalling.

XIc. Some Logical Difficulties In The Interpretation Of Apparent Deception.

Descriptions of food calling in chickens (Gyger and Marler, 1988) provide an intriguing potential case of active deception. Cocks were reported to food call while holding inedible objects, and to do so preferentially when hens were distant and hence less likely to detect the prevarication. Laboratory studies analysing the conditions of food call production have demonstrated that, at least under controlled conditions, this vocalization is elicited specifically by food (Evans and Marler 1994). Playback experiments have revealed that food calls are sufficient to elicit anticipatory feeding movements. Food calls thus have properties that satisfy both production and perception criteria for functional reference. Are we then required to conclude that selective calling by chickens provide an unambiguous example of deception in the cognitive sense?

There are both technical and logical deficiencies in the Gyger and Marler (1988) analysis that suggest such an interpretation would be premature. The data were obtained from opportunistic recordings of five cocks maintained in large pens. Statistical analyses were then performed with degrees of freedom determined by the total number of calling bouts (108) rather than the number of subjects (5). This is an example of the 'pooling fallacy' (Machlis et.al., 1985;

Martin and Bateson, 1993) in which the degrees of freedom are substantially inflated and the risk of Type I error is likely to be higher than the stated alpha level (but see Leger and Didrichsons, 1994). More conservative analyses would not have sufficient statistical power to demonstrate that the males, as a group, food called ‘deceptively’ more often when hens were distant than when they were close. An additional concern about this data set is that each of the subjects did not contribute equally to the analysis: two of the males yielded almost 76% of the data. What remains is thus essentially an anecdotal account describing the vocal behaviour of two birds. Like other such descriptions of deceptive behaviour (Whiten and Byrne, 1988; Byrne and Whiten, 1990, 1991), this is a thought-provoking example, but it does not establish that deceptive food calling is a property of chickens as a species, or even that it was a reliable phenomenon in the group under study.

Descriptions of natural vocal behaviour also illustrate some of the logical problems that confront us in making a case for cognitive deception. Consider the observation of a cock food calling with an apparently inedible object such as a twig. Human observers would clearly be disposed to class this as a non-food object and to regard the calling as a potential case of deception. There is, however, a real risk that this decision reflects more about human language, culture, and categorization by the observer than about the way in which objects are classified by the birds. It will be important to determine how cocks treat the apparently ‘inedible’ objects that they sometimes manipulate while food calling. If such objects are subsequently ingested, even though they have modest nutritive value, it will be reasonable to assert they are categorized as palatable by the birds and that, even though they may be less preferred than other objects, such as live invertebrates, they nevertheless qualify as ‘food’. Much more thorough descriptions of the feeding behaviour of galliforms will be required before we can discriminate ‘honest’ from ‘deceptive’ calling. It will be essential for this distinction to be based upon the animals’ categorization scheme rather than those that human observers bring to the problem.

A second logical difficulty with interpreting putative instances of deceptive signalling is suggested by the literature on animal learning. Recent experiments employing instrumental conditioning techniques suggest strongly that contextual conditioning of food calling occurs. Birds were trained to work for food by pecking a hinged plastic key, which was illuminated from behind with a red light (Evans and Marler, 1994). In the first part of each test session, this light was switched off and the key was inactive. After two minutes, the light was switched on, signalling to the bird that pecks delivered to the key would produce food on a fixed ratio schedule (each bout of 16 pecks triggered a delivery of 3 small food pellets). Birds were initially unresponsive to the red light, which they had not previously experienced. Over the course of training, they rapidly learned to approach and to begin pecking as soon as the key was illuminated. After several such sessions, birds would engage in obvious foraging behaviour (e.g., scratching and pecking at the ground) as they moved toward the response panel. They also food called as soon as the light was turned on. Later still, birds began food calling when first introduced into the test cage. Some individuals even began food calling when they were removed from their home cage and placed in a canvas bag to be weighed at the beginning of each test. None of these procedures had elicited food calling prior to training. These observations suggest that environmental cues reliably associated with the discovery of food can become sufficient to evoke food calling.

The possibility of contextual conditioning complicates the interpretation of food calling in the absence of food under natural conditions, because birds may well have been vocalizing in a location where food had previously been discovered. The implications of this are most easily illustrated with a hypothetical example of human behaviour. Imagine two people (A and B) on a long-distance drive. They have not eaten for several hours. Person A spots a roadside billboard advertising a fast food restaurant at the next motorway exit and exclaims, “Food!”. Clearly A does not have a food item, but rather is responding to an environmental cue that

reliably predicts feeding opportunities. It is possible that B would entertain doubts about A's gastronomic judgment, but it is unlikely that they would consider their companion to be behaving *deceptively*. The implication of this logic is that a compelling case for deception will require an analysis not only of the immediate circumstances of signal production, but also of historical context (Smith 1977, 1981, 1991), that is, of the animal's prior experience of pairings between the environmental events that normally elicit a call and the other stimuli reliably present at the time of production.

A final point that arises from the Gyger and Marler (1988) study concerns the frequency of 'deceptive' signalling. It was claimed that fully 45% of food calls were deceptive. This estimate is based on a flawed statistical analysis (see above), and the actual value may well be somewhat lower. Nevertheless, there is a striking contrast with classical theoretical analyses of animal signalling which suggest that 'deceptive' usage should be rare (Dawkins and Krebs, 1978). It is often assumed that this is a general rule in animal communication, so that claims for deceptive signalling at an appreciable rate are inherently not credible. Many of the original analyses of deceptive signalling were, however, based upon game theory models of aggressive interactions in which the costs of deception (severe physical injury) are potentially very high (Maynard Smith and Price, 1973; Maynard Smith, 1982). The payoff matrices describing signalling behaviour such as food calling are almost certainly quite different. It is intriguing to note that in instrumental conditioning paradigms, animals will continue to work on very 'lean' schedules of reinforcement. Under these conditions, less than one response in a hundred might produce a delivery of food. This analogy suggests that, under more natural conditions, animals might be prepared to expend energy (e.g., by approaching a sender) even if the link between the sender's behaviour and feeding opportunities has been quite tenuous. There is a real need for systematic studies of signal reliability with the goal of establishing the range of values that animals naturally experience for the correlation between signal production and presence of the putative referent.

XII ULTIMATE QUESTIONS

This will be a short section. I have so far been concerned almost exclusively with proximate questions, not because I regard them as more interesting or more important than evolutionary ones, but because this has been the principal focus of most studies conducted to date. Work on referential signalling has been comparative only in the weak sense (Wasserman, 1993) of evaluating the characteristics of animal signals to determine whether they have properties in common with language. This strategy has generated a number of important findings, some of which call into question traditional assumptions about the degree to which humans are unique. Dogmatic statements about the special attributes of language have perhaps been particularly tempting targets because they can successfully be attacked with a very modest data set; logically a single contradictory result will suffice. But there have been no studies of referential signalling that are comparative in the strong sense, providing a series of systematic analyses of closely-related species that would permit us to reconstruct the evolution of a trait, as has been done successfully in studies of sexually-selected signals (e.g., Ryan and Rand, 1993; Basolo, 1995a,b).

XIIa. Evolution Of Referential Signals

Some clues about the way in which comparative studies might proceed are provided by comparisons between the alarm call systems of ring-tailed and black-and-white ruffed lemurs. These two species have quite different behaviour and ecology. Ring-tailed lemurs are highly terrestrial and occupy open habitat (e.g., Jolly, 1966; Tattersall, 1982), while ruffed lemurs are arboreal and live in dense rainforest (Pereira et al., 1988). Ring-tailed lemurs produce highly-specific alarm calls, both during natural encounters with predators and during experimental simulations of such events. Playback experiments demonstrate that call type encodes sufficient

information for companions to select appropriate responses (Macedonia and Polak, 1989; Macedonia, 1990; Macedonia and Yount, 1991; Pereira and Macedonia, 1991). Ruffed lemurs react to approaching predators with a graded series of calls which, like the alarm calls of ground squirrels and marmots, have only a probabilistic association with predator class. Consistent with these studies of call usage, playback experiments with ruffed lemurs do not reveal qualitatively different responses to different types of alarm call.

Ring-tailed lemurs share with vervet monkeys the traits of living in an open habitat and of spending a great deal of time on the ground. The transition from an arboreal to a largely terrestrial existence probably produced a substantial increase in predation risk. This factor is, however, clearly not sufficient to account for the characteristics of the ring-tailed lemur alarm call system, because there are many other species of small mammals (e.g., sciurid rodents) that are also exposed to frequent attacks from terrestrial predators but have rather less specific alarm calls. It has been suggested that one selection pressure for the evolution of referential alarm calls may have been the use of qualitatively-distinct and incompatible strategies for avoiding different classes of predator (Macedonia and Evans, 1993). Squirrels avoid both coyotes and hawks by running toward a burrow, and their alarm call system seems to provide information that allows receivers to assess the time available for such a response. Vervets and ring-tailed lemurs have the shared characteristic that responses to avian predators involves movement into dense cover, while the safest refuge from ground predators is the outermost branches of trees (a location where vulnerability to attack from raptors is actually increased). Such ecological factors may have played a role in the evolution of alarm call systems that designate predator class (Macedonia and Evans, 1993).

XIIb. Habitat Characteristics And Predator Recognition

Differences in ecology have also been implicated as one determinant of signal specificity. Studies of alarm call production under naturalistic conditions suggest that chickens respond to a fairly broad array of overhead objects (e.g., Gyger et al., 1987). Subsequent laboratory studies revealed that the size and speed of a simulated predator (Evans et al., 1993b) play an important role and that there is also a degree of sensitivity to shape and spatial location. Alarm call production in chickens is nevertheless substantially less highly-specific than that of some other birds. For example, studies of alarm calling by lapwings (Walters, 1990) demonstrate that both South American and African species make subtle discriminations between raptors that are visually very similar. Lapwings inhabit open terrain and this probably affords them the opportunity to examine approaching raptors for some time before producing an alarm. In contrast, red junglefowl, which are the ancestral species for domesticated chickens (Fumihito et al., 1994), live in forest and dense brush where visibility is typically limited (Collias and Collias, 1967) and the time available for responding to potential avian predators will consequently be brief. This ecological constraint may have selected for a simple rule of thumb for predator recognition which, although it entails some loss in accuracy, facilitates rapid response. Other reports describing the anti-predator behaviour of forest-dwelling birds also suggest a fairly high frequency of false alarms (Trail, 1987).

Although the evidence remains fragmentary, the results so far available are consistent with the idea that the specificity of alarm calls has been shaped by habitat characteristics. It is possible that the range of events evoking alarm calls is the product of a trade-off between the rate of Type I errors (i.e., calling when the approaching bird is not dangerous) and Type II errors (i.e., failing to respond to an approaching predator) over evolutionary time (Evans et al., 1993b). Birds living in open habitats may have been subject to selection for low Type I error rates, as the cost of the frequent false alarms that would otherwise be produced in an environment where aerial objects are visible much of the time would be prohibitive. This process would give rise to relatively specific alarm calls. Species inhabiting habitats where visibility is restricted and response times must be short may have been selected to reduce Type

II error rates and their alarm calls may be less specific as a consequence. The logic of this argument is closely analogous to that of classical signal detection theory (e.g., Swets, 1961).

The theoretical ideas outlined above about the factors responsible for the evolution of referential signal systems (Macedonia and Evans, 1993) and about the relationship between habitat characteristics and signal specificity (Evans et al., 1993b) remain highly speculative. They do, however, both make clear predictions and are thus amenable to empirical test. This will require comparative studies with a focus upon groups of species selected either to have reliable differences in their strategies for avoiding predation, or to have similar anti-predator behaviour, but different habitat characteristics.

XIII CONCLUSIONS

We have learned a great deal about referential signals in the three decades since Struhsaker's pioneering studies of vervet monkeys (Struhsaker, 1967). In striking contrast to traditional assumptions about the affective nature of animal communication, it is now clear that both non-human primates and birds are capable of producing relatively specific alarm calls in response to approaching predators and that the information encoded in such signals is sufficient for companions to select appropriate responses. These systems have the property of functional reference. The discovery of referential signalling extends the parallels between the properties of human language and those of the natural behaviour of non-human animals (Marler et al., 1992; Snowdon, 1993a; Evans and Marler, 1995). This is valuable because it provides an empirical basis for discriminating between those aspects of language that really are uniquely human and others that are more widely shared, and possibly quite ancient.

The discovery that non-human primates possess a communicative system with a surprising degree of flexibility and complexity has encouraged exploration along the lines of Griffin's suggestion (Griffin, 1981, 1984, 1992) that signalling behaviour provides a potential window on the mental life of animals. This work has involved grappling with a series of difficult philosophical problems, such as the extent to which animal signals may usefully be viewed as deceptive, and whether monkeys attribute knowledge or ignorance to their companions (Cheney and Seyfarth, 1990). While these are undoubtedly important issues, I suggest that they are likely to prove recalcitrant. Specifically, I have argued that it will be difficult to build a logically-impregnable case for cognitive deception (XI), and that the current evidence does not require us to conclude that the effects of signals are mediated by mental representations of the eliciting event (X).

The focus on communication as a vehicle for analyzing complex cognitive processes has necessarily meant that a number of other issues have remained unaddressed. Analyses have been principally concerned with variation at the level of signal class. We have quite detailed descriptions of the factors determining signal type during production, and of the responses evoked, but we know much less about the significance of fine-grained variation in the structure of referential signals (VII). It is likely that this reflects the interplay of stimulus attributes and motivational state (Marler et al., 1992), and it will be particularly important to determine whether there are aspects of signal morphology that reflect either of these factors independently.

The design of referential signals cannot be accounted for by considering just the physical properties of eliciting stimuli (VIII). This is most obviously true if we are concerned with explaining morphology in a broad sense, taking into account not only short-term variation in acoustic characteristics but also the time-course of calling. Signal properties are likely to have been influenced by a long list of factors. These include the physical environment, the sensory attributes of receivers (which dictate the structural correlates of the requirement that signals

encoding very different types of information should be readily discriminable), and design for effect over distances that may be quite short in some cases (e.g., aerial alarm calls) and considerable in others (e.g., ground alarm calls). In addition, we must consider the possibility that the various signals in a given repertoire may be designed to influence the behaviour of different sets of receivers, so that some calls address only close companions while others also target heterospecifics such as an approaching predator.

Any complete account of communication will need to incorporate the effects of contextual factors (IX). Analyses that examine only environmental events, such as the discovery of food or the approach of a potential predator, will fail to predict accurately the probability of calling in systems where signal production is sensitive to the nature and presence of an audience. The responses of receivers are almost certainly also influenced by contextual cues, which are available both from the non-signalling behaviour of the sender synchronous with call production and from relationships between signals and environmental events over much longer periods. The responses that we observe in natural social interactions are thus likely to reflect the integration of information from signals and from the contexts in which they are produced, but there have been very few experimental analyses of this process. If contextual cues prove to be important determinants of the responses evoked by referential signals, then this will imply that associative learning plays a larger role than is envisaged by current theory.

We do not currently have a comprehensive model of any system of referential signals. I suggest that providing one is a worthwhile goal. This will not be a trivial undertaking because it will require a series of complementary analyses at different levels (Fig. 1). It will be necessary to consider not only the meaning of call types, but also fine-grained variation within signal class. We will also have to expand the time scale of our studies, so as to encompass behaviour other than the initial response to an event, taking into account the possibility of long-term (tonic) effects. The development of referential signals will require further study, building on the evidence for plasticity in signal production and enquiring whether this is also true of the responses evoked. Finally, it will be essential to understand the effects of those social factors that modulate both the probability of calling and the behaviour of receivers.

There are at least partial answers to some of these questions, but they have been obtained in relative isolation. We now have an opportunity to begin integrating the available findings, while at the same time identifying and addressing the remaining lacunae in our knowledge. By proceeding in this way we will be able to place referential signalling in the wider context of other social behaviour, to account for signal design, and, in particular, to explore the fitness implications of some of the phenomena that we now understand at the level of mechanism.

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