Chapter 7

INCIDENTAL EMISSIONS, FORTUITOUS EFFECTS, AND THE ORIGINS OF COMMUNICATION

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ABSTRACT

In recent years, a small group of animal behaviorists has been calling for a renewed focus on proximate mechanisms in the study of behavioral evolution (Kennedy, 1992; Stamps, 1991). These calls have been made to counter the current view, implicit in most contemporary analyses of animal behavior, that we can understand ultimate causation without worrying about the mechanistic details. As noted by Stamps (1991), however, today's "students of ultimate causation in behavior have begun to 'rediscover' the importance of proximate mechanisms" (p. 342). Specifically, there is a growing realization that proximate mechanisms are not mere details—rather, they vitally shape our understanding of function and of the evolutionary origins of behavior and structure.

Communication is an area of animal behavior, we argue, that can especially benefit from a renewed focus on proximate mechanism. This argument is

developed as follows: (1) Students of animal communication have tended to make preliminary assumptions of function when confronted with novel signals; (2) these assumptions of function have steered us away from studying the proximate mechanisms that underlie signal production; and (3) by assuming function and ignoring mechanism, we arrive at a distorted view of the communicatory relations between senders and receivers and, in addition, deny ourselves a path to understanding the evolutionary origins of communication. This argument is supported by examples of how appropriate emphasis on mechanism broadens and deepens our understanding of communication.

INTRODUCTION

> ...theories of behavior which ignore problems of origin can scarcely be called complete.
> —M. T. Ghiselin (1969, p. 208)

Judith Stamps (1991) has recently noted that a resurgence of interest in proximate causation is benefiting the study of ultimate causation in animal behavior. Such a resurgence in the study of mechanism, she argues, is necessary to balance the explosion of research in behavioral ecology and sociobiology of the last 20 years, research that has focussed predominantly on ultimate causation. Many examples are provided in her article that illustrate the ways in which the study of mechanism can further the study of evolution, but none is directly related to the topic of animal communication. The aim of this paper is to examine the applicability of Stamps' perspective to the field of animal communication.

At any given time, a particular organism possesses a variety of anatomical features, some of which are adaptive and some nonadaptive. The same is true for behavioral features, including vocalizations and other acoustic behaviors. Animal vocalizations are produced by a diversity of physiological and biomechanical mechanisms, and they are also diverse with respect to the degree to which they have been modified by the evolutionary process. At one extreme are vocalizations that affect the behavior of other animals and have been modified for communication. At the other extreme are many vocalizations that are emitted as incidental by-products of other mechanisms (e.g., sneezes, coughs), that are ignored by other animals, and have not been modified for communication.

Thus, one goal of the study of acoustic communication should be to understand the evolutionary processes by which incidental vocalizations are modified and incorporated into a communicatory system. To achieve that goal, we should follow Stamps' suggestion and elevate the importance of proximate mechanism in the study of communication. By doing so, we will correct for the tendency of current perspectives to distort the relative contributions of senders and receivers to communicatory systems. Specifically, senders (i.e., animals that

are, at any given moment, emitting information) are often conceptualized today as the primary communicatory actors while receivers (i.e., animals that are, at any given moment, processing information) are conceptualized as passive participants. On the contrary, we argue, receivers are equal participants in communicatory systems who often act as selecting agents on the varied signals to which they are exposed.

Although Darwin founded the scientific study of the evolution of communication, he did not himself fall into the habit of assuming that every novel vocalization had a communicative function. In fact, he cautioned against such assumptions. For example, in *The Descent of Man, and Selection in Relation to Sex* (1871/1981) he writes: "Animals of all kinds which habitually use their voices, utter various noises under any strong emotion, as when enraged and preparing to fight; but this may merely be the result of their nervous excitement, which leads to the spasmodic contraction of almost all the muscles of the body, as when a man grinds his teeth and clenches his hands in rage" (p. 275).

Even today, Darwin's clarity and grasp of parsimony are remarkable. In effect, his appeal is for initial consideration of the possibility that a vocal emission is an acoustic by-product of physiological or biomechanical forces, rather than assuming that each sound has a communicatory function. Of course, considerations of function and mechanism are not mutually exclusive. Nonetheless, we can no longer sanction the current imbalance with regard to the study of function and mechanism (Kennedy, 1992). When we ignore mechanism, we blind ourselves to evolutionary history.

After Darwin, other theorists have cautioned against the "unwarranted uses of the concept of adaptation. This biological principle should be used only as a last resort. It should not be invoked when less onerous principles, such as those of physics and chemistry or that of unspecific cause and effect, are sufficient for a complete explanation" (Williams, 1966, p. 11).

Williams contrasts adaptations with what he variously calls "fortuitous relationships," "incidental consequences," and "by-products." Of course, many of these by-products confer a survival advantage, but that is not sufficient for them to qualify as adaptations: "In an individual organism an effect should be presumed to be the result of physical laws only, or perhaps the fortuitous effect of some unrelated adaptation, unless there is clear evidence that it is produced by mechanisms designed to produce it" (Williams, p. 261).

But what do we call those by-products that have come to be shaped by natural selection for a new function? For example, the feather insulation of birds has been referred to as a "preadaptation" for flight, a term whose teleology detracts from its explanatory usefulness. Gould and Vrba (1982) correct for this temporal distortion of language by suggesting that, in the above example, we should speak of feathers as "exaptations" for flight, by which they mean that although feathers are fit for their role in flight they were not originally selected for that role.

Forty years ago, Morris (1956) drew attention to the ways in which the feathers of birds are also used in a variety of ways as communicatory signals. In some cases, he argued, feather postures have become specialized as signals in that the "original motor patterns concerned have been modified in any way in connection with their new secondary function" (p. 82). In other words, feathers have not only been exapted for flight but, in some species, for communication as well.

The above discussion illustrates how a number of theorists have emphasized the importance of distinguishing between functions and effects. As we discuss in the next section, failure to make this distinction distorts the relative contributions of senders and receivers and thus makes the evolution of communicatory systems more difficult to understand.

THE DYNAMIC RELATIONS OF SENDERS AND RECEIVERS

Deciding on a definition of communication on which a majority of researchers can agree has proved to be a difficult task. Most broadly, we might, as Smith (1977) preliminarily suggests, "define communication as any sharing of information from any source" (p. 13). To this broad definition, any of a number of restrictions may be added (see Burghardt, 1970, for a review and analysis of such restrictions). For example, one might insist that a communicatory signal alter "the probability pattern of behavior in another organism... from what it would have been in the absence of the signal" (Wilson, 1975, p. 176). Burghardt (1970) argues that a communicatory act must be intended to communicate, where "intent can be looked at scientifically merely by considering that it is to the real or perceived advantage of the signaler or the signaler's group for it to get its message across to whatever organism is involved" (p. 12). In addition, one might insist that the signal be specialized for communication, or that the communicatory system be adaptive for the sender and/or the receiver. Finally, some may even wish to restrict communication to exchanges between members of the same species.

A consensus on a single definition of communication has not been reached for several reasons, one of which is that no unambiguous boundary on the continuum from incidental by-product to communicatory signal has yet been located. This ambiguity arises from the fact that the relations among senders and receivers are complex, comprising a dynamic system of multiple components interacting in diverse ways (Kelso, 1995; Thelen and Smith, 1994). As a result, the "cause" of a communicatory system cannot be localized in any single component of that system. Just as organismal development arises from the dynamic interactions between the organism and the environment (Oyama, 1985), communication arises from the dynamic interactions between sender and receiver.

Recent definitions of communication have tended to focus on the sender. But any attempt to define communication exclusively in terms of the sender is

doomed because no acoustic signal can acquire an adaptive function unless a receiver can detect it and process the information in an appropriate way. For example, stingless bees emit an audible (to humans) hum while flapping their wings during warmup and, moreover, the frequency of the hum is directly correlated with thoracic temperature (cited in Heinrich, 1979, p. 56). In other words, the hum is informative. But is the information contained in this sound emission of biological interest to any animal other than the entomologist interested in the thoracic temperature of bees?

As another example, the rattle of rattlesnakes could potentially alert conspecifics to a dangerous situation. The rattle's sound energy, however, is concentrated above 2000 Hz while rattlesnakes are most sensitive to sounds below 700 Hz; these and other facts suggest that rattling is not important for conspecific communication (Fenton and Licht, 1990). In this case, the potential for communication exists, but conspecific receivers have proven ill-equipped to detect or process the information. On the other hand, rattling does incidentally provide valuable information about rattlesnake size and dangerousness to ground squirrels aggressively defending their young against a snake (Rowe and Owings, 1990, in press; Swaisgood, 1994).

Thus, while there are an infinite number and variety of signals being emitted at any given time, these signals can only begin to develop a communicatory function, and their communicatory significance can only be assessed, when they elicit responses from receivers. As an example of a well-accepted communicatory behavior, consider the "mating call" of male field crickets of the genus Gryllus. In response to this call, female crickets approach the male and mating ensues. This call alters the female's behavior, it confers a reproductive advantage to the male, and it is intraspecific. Thus, we might tentatively describe this interaction as the male cricket communicating to the female or, in the language of Krebs and Dawkins (1984), manipulating her.

One's comfort with such descriptions is challenged somewhat when one considers that parasitoid flies of the genus Ormia also move toward calling male crickets but, in their case, they deposit their offspring on or near the male. The offspring then burrow inside the cricket, grow, and eventually kill their host (Robert et al., 1992). As Krebs and Dawkins (1984) point out, "most people would not wish to say that the crickets were signalling to the flies... because most authors agree in wanting to exclude such incidental consequences" (p. 380). After all, it is argued, the male cricket did not intend (in Burghardt's sense) to attract the fly or, in other words, the male cricket's song was not designed by natural selection for attracting the fly.

From the female cricket's perspective, responding to the male's song provides her with an opportunity to mate and thus increase her reproductive fitness; she is taking advantage of information in her environment and manipulating the male cricket for her own ends. Similarly, the parasitoid fly is taking advantage of information in her environment and ensuring her own reproduction

at the expense of those crickets that are unlucky enough to attract the flies by singing. But the fly's response is not mere happenstance. On the contrary, natural selection has provided her with a hearing organ that is tuned to the male cricket's song and is unique in its convergence upon a design that "more resembles a cricket's ear than a typical fly's ear" (Robert et al., 1992, p. 1135). In other words, the female fly's ear is specialized for detecting the male cricket's song.

If we attempt to define communication from the sender's perspective alone, we will be forced, like Krebs and Dawkins (1984), to argue that the male cricket is communicating with the female cricket but not with the female fly. But, on what objective basis do we conclude that the specialization of a sender's signal is indicative of communication while specialization of the receiver's detection apparatus is not? Are they not two equally effective means by which senders and receivers establish a communicatory relationship? We believe they are.

If it is acknowledged that senders and receivers both participate fully and actively in the communicatory process, it is then only a small step to acknowledge that specialization of either participant equally qualifies as an important feature of communication. Thus, we are arguing that communication is not the product of any single privileged participant but emerges from the relations and interactions among senders and receivers. Senders and receivers are both necessary for the formation and maintenance of communicatory systems, where maintenance includes both positive and negative forces acting on each contributor's behavior. Acceptance of this view will not, however, make us feel any less uncomfortable about stating that the male cricket is communicating to the fly; this lack of comfort is in part a result of our natural tendency to anthropomorphize and insist that no right-thinking cricket would actively call out to its executioner (see Kennedy, 1992, for a detailed discussion of these anthropomorphic tendencies). But, if we step back and view the system in its entirety, we see that female crickets and flies are acting similarly and, each in their own way, contributing to the dynamics of this communicatory system.

Specialization, of a sender's signal or a receiver's detection apparatus, can only occur after senders and receivers have entered into a relationship. Thus, although sounds may be produced incidentally at first (as in the stingless bee), in time they may come to be specialized for sound production. On the other side of the coin, but much less well examined or understood, are the incidental responses of receivers to various signals. For example, Tungara frogs (Physalaemus pustulosus) emit vocalizations composed of two components, a 'whine' and a 'chuck' (Ryan et al., 1990). Female Tungara frogs prefer males that emit chucks of lower frequencies; lower frequency chucks signal a male of larger body size. But females of a related species, P. coloradorum, also prefer calls that contain chucks even though the calls of conspecific males do not contain chucks.

Similarly, and in the visual modality, the preference of the females of one species of freshwater guppy (Xiphophorus helleri) for males with large swordtails may have originated in a bias of the sensory system of ancestral fish before

the swordtail evolved (Basolo, 1990). This view is supported by the finding that females of a related but swordless species (X. maculatus) also prefer males with swordtails. Although there is disagreement regarding the phylogenetic relations between the swordless and sworded species (Pomiankowski, 1994), the role of sensory bias in signal evolution deserves far more attention than it has received thus far (Guilford and Dawkins, 1993).

ANSWERS FIRST, QUESTIONS SECOND

When Krebs and Dawkins (1984) state that "most of the sounds given off by [animals] are best interpreted as being adapted...to influence the behaviour of other animals" (p. 380), they are expressing a commonly held view among communication researchers. We have argued above that this assumption of communicatory function blinds us to mechanism and, in turn, to evolutionary history. As we argue below, this assumption has yet another, but related, drawback.

Practitioners of comparative psychology, ethology, behavioral ecology, and sociobiology share the view that naturalistic contexts give meaning and significance to behavioral phenomena. Thus, it is common practice today that when a vocalization is detected, a researcher next determines the contexts in which the vocalization is emitted and the behaviors that accompany it. Based on this information, a functional hypothesis is formulated that relates the emission of the vocalization to the context in which it is emitted. For example, a vocalization may be discovered that is emitted by males during the mating season, a discovery that would suggest that the vocalization functions as a sexual attractant. Similarly, a vocalization may be emitted when two males meet in an aggressive encounter, thus suggesting a role for this vocalization in the modulation of aggression. What is important here is that it requires very little imagination to hypothesize a communicatory function for a newly discovered vocalization.

As one example of the progression from the discovery of a vocalization to the suggestion of a communication hypothesis, consider the "cackle" of male Japanese macaques (Macaca fuscata): "Males cackle only during copulations. These rhythmic calls, occurring before, during and after thrusting at various times, and also while the female is cackling and copulating, may serve to strengthen the pair bond and possibly hasten the culmination of a mating sequence" (Green, 1981).

The existence of a stereotyped vocalization that can be recognized and categorized, coupled with its regular appearance in a particular setting (physical and social), is generally sufficient to inspire a communication hypothesis. In the above case, the discovery of a vocalization within a copulatory context implied

a communicatory function for the vocalization and thus drove the suggestion of two possible functions.

This example provides insight into the question-and-answer process as it often exists in the study of animal communication. The suggestion that the cackle of the Japanese macaque "may serve to strengthen the pair bond and possibly hasten the culmination of a mating sequence" is based upon observation of the context in which the vocalization is produced—no observation is reported that these macaques form stronger pair bonds or mate faster than related species that do not cackle. Viewed as an analytic strategy, the researcher invented problems for the animal (i.e., need to strengthen the pair bond, need to hasten the culmination of the mating sequence) for which the vocalization was to be a solution.

The sneeze-like Snough vocalization of golden lion tamarins (Leontopithecus rosalia) provides another example. McLanahan and Green (1977) write that the Snough "sounds very similar to a sneeze. Its frequent occurrence at the end of feeding and locomotor bouts leads us to postulate that it may communicate completion of an activity" (p. 262). While golden lion tamarins may emit the Snough after completing particular activities, the potential benefit of communicating that fact is not addressed. Nor is any evidence provided that the behavior of conspecifics changed at the end of feeding or locomotor bouts. On the other hand, if such observational data had been offered, and if the behavioral changes seemed well-timed, then a search for such a timing mechanism would be reasonable.

In contrast, there are examples of vocalizations that, when discovered, have provided clear explanations for unexplained phenomena. For example, researchers noticed that large groups of Asian elephants often display coordinated behaviors despite the absence of a detectable signal. The riddle of this coordinated behavior was solved when it was discovered that these elephants emit infrasonic vocalizations (i.e., vocalizations below the range of human hearing) and that these vocalizations are emitted immediately prior to the coordinated movements of multiple elephants (Payne et al., 1986). Unfortunately, the significance of "the remarkable coordination" (Poole et al., 1988, p. 386) of elephants is still unclear. Nonetheless, this history provides a nice example of a clearly defined question generating the search for a solution.

These examples demonstrate the practical difference between searching for an answer to a question versus searching for a question to an answer. When questions are stated clearly (e.g., "What signal triggers the coordinated movements of elephants?"), we can imagine what the answer to the question will look like, and can map out a series of experiments with a clear terminus. In contrast, when we search for a question to an answer ("The Snough vocalization of golden lion tamarins is important for X"), our search may never terminate. Thus, when questions come second, there are serious consequences for the form of the scientific approach that emerges.

ANALYSES OF ACOUSTIC COMMUNICATION IN RODENTS

Thus far, we have detailed the potential pitfalls of assuming communicatory function and ignoring mechanism. Now the time has come to explore how considerations of mechanism broaden our understanding of the origins of communication. We will do this in the next section by providing examples of signals that are produced as incidental by-products of a diverse array of production mechanisms. In this section, we summarize our own work on the vocalizations of newborn and adult rats.

In our investigations of the vocalizations of Norway rats (Rattus norvegicus), we have set aside issues of communicatory function and have concentrated instead on the mechanisms responsible for the production of these vocalizations. To illustrate this approach and its benefits, we discuss three broad categories of rodent (mostly ultrasonic) vocalizations, all of which have received a great deal of experimental attention: the "distress calls" of newborn rats, the "short calls" of the adults of many rodent species during strenuous activities, and the post ejaculatory "long calls" of adults. In each case we show that attention to the mechanisms that produce and constrain these vocalizations enhances our understanding of their evolutionary history and communicatory significance.

"Distress Calls" of Rodent Young

The newborns of many rodent species emit ultrasonic vocalizations when they become cold following isolation from the nest (Zeppelius and Schleidt, 1956; Noirot, 1972). The fact that rodent young with limited thermoregulatory abilities emit these vocalizations when they are çold, and the fact that rodent mothers often respond to these vocalizations by retrieving the pup to the warm nest (Allin and Banks, 1972) or relocating the site of a disturbed nest (Brewster and Leon, 1980), have led many to conclude that the function of these "distress calls" is to elicit maternal care and protection. Given the remarkable fit between the behavior of the pups, its physiological needs, and the response of the mother, this seemed like a reasonable conclusion.

We noted, however, that although the effects of cold on this vocalization had been studied (Okon, 1970, 1971), there had been no attempt to relate ultrasound emission to the pup's other well-known physiological responses to cold. These responses include nonshivering thermogenesis via the activation of brown adipose tissue (BAT), an organ specialized for heat production. We hypothesized that if the vocalization is a component of the pup's overall response to cold exposure, then we might find that ultrasound emission and heat production by BAT are initiated at the same time.

Contemporaneous activation of BAT and ultrasound emission during cold exposure did occur, and was accompanied by an increase in oxygen consumption and the expression of a unique respiratory pattern characterized by prolonged expirations (Blumberg and Alberts, 1990; see also Blumberg and Stolba, 1996, for a recent update on this earlier work). The ultrasound occurred during these prolonged expirations, as had been demonstrated earlier (Roberts, 1972). This concurrence of ultrasound emission and prolonged expiratory duration suggested to us that the cold-exposed rat pup, like other mammalian newborns, employs a respiratory mechanism called laryngeal braking that helps maintain lung infla- tion. Laryngeal braking involves the constriction of the larynx following inspi- ration, resulting in prolonged expiratory duration and enhanced gas exchange in the lungs. In this context, any sound produced by the combination of laryngeal constriction and increased intrathoracic pressure is a by-product of expiration against a constricted larynx, as is the audible "grunt" emitted by human infants and lambs during laryngeal braking (Harrison et al., 1968; Johnson et al., 1977).

As we pursued this line of reasoning, new insights were gained. First, we used manipulations that presumably cause distress (i.e., starvation, hypoxia) but that inhibit physiological responding to cold (Blumberg and Alberts, 1991b). Cold-exposed pups that were starved or hypoxic did not activate nonshivering thermogenesis and they also did not ultrasound, suggesting that the vocalization is not simply a distress response. Second, with our physiological perspective, we revisited the issue of the vocalization's proximate stimulus and were able to demonstrate that the vocalization is specifically modulated by thermal and respiratory factors as opposed to factors more broadly defined as anxiety-related (Blumberg et al., 1992a, b). Remarkably, pups even emit the vocalization during recovery from deep hypothermia at body temperatures so cold that motor behavior is prevented (Hofer and Shair, 1992). These results suggest that extreme caution should be exercised by those suggesting the use of the ultrasound-pro- ducing rat pup as an animal model for human infant separation anxiety.

There is currently no evidence that the rat pup's vocalization or laryngeal apparatus is specialized for communication (Roberts, 1975); such evidence would provide support for the hypothesis that the vocalization is an adaptation or exaptation for communication. But we do know that while pups are deaf to their own vocalization at ages when they are emitting it most often, the mother's hearing curve is tuned specifically to the pup's vocalization frequency; this is also true for a number of other rodent species including the house mouse (Mus musculus) and the red-backed mouse (Clethrionomys glareolus; Brown, 1973). Thus, selective pressure on the mother's hearing sensitivity and propensity to retrieve pups may have been more significant than the selective pressure on pups to modify their ultrasonic emissions during isolation from the nest. This perspec- tive does not rule out the possibility that ultrasound production elicited by cold exposure can be modulated by nonthermal factors such as olfactory and tactile cues from the mother. Such modulation may very well occur, especially in older

pups and for brief durations (Hofer et al., 1993, 1994). More work is needed, however, in which the physiological consequences of such stimuli are more carefully measured and controlled.

We conclude that pup ultrasound is emitted as an incidental by-product, it is a reliable and informative indicator of a cold and metabolically active pup, adult rats can detect the vocalization, and the pup's mother often responds to this vocalization by retrieving the pup to the warm nest. Moreover, we suggest that this is a richer, more concrete, and less mentalistic description of the interaction between pup and mother than that which states that isolation from the nest causes anxiety and/or distress in the pup who is then motivated to cry out for maternal retrieval to the nest.

Vocalizations Associated with Arousal and Locomotion in Adult Rodents

Many rodent species emit ultrasonic or audible pulses during mating and other contexts involving high levels of arousal. For example, during copulatory behaviors, male and female collared lemmings (Dicrostonyx groenlandicus) emit an ultrasonic 'twitter' (Brooks and Banks, 1973) and male and female rats (Rattus norvegicus) emit a 40–70 kHz vocalization (Thomas and Barfield, 1985). For these species, and for many others, a number of communicatory functions have been hypothesized for these vocalizations; these hypothesized functions include facilitation of female receptive and/or proceptive behaviors and the inhibition of female aggressive behaviors during copulation.

A cursory examination of reports on these 'mating calls' reveals a curious association between these emissions and the animals' locomotor behaviors. This association has only been studied in detail for the ultrasonic vocalization of the Mongolian gerbil (Meriones unguiculatus; Thiessen and Kittrell, 1979; Thiessen et al., 1980). This vocalization is emitted during different modes of locomotion, all of which involve the landing of the forepaws on the ground. Thiessen and his colleagues attributed the emission of sound to the forcible expulsion of air through the larynx as a result of physical compression of the lungs during landing.

That vigorous locomotor behaviors, in which the forepaws land forcibly on the ground, are associated with the emission of sound is not surprising when one considers the biomechanics of locomotion in rodents and other mammals (Bramble, 1989; Blumberg, 1992). In addition, mammals typically time footfall patterns and respiration in such a way that expiration occurs as forelimbs strike the ground (Bramble and Carrier, 1983). These and other considerations suggest that, at least in some cases, the ultrasonic vocalizations associated with locomotion in sexually active rodents, as well as those vocalizations occurring in other contexts (e.g., during pelvic thrusting in mice and hind foot thumping in gerbils; Sales, 1972), are acoustic by-products of biomechanical stress and thoracic compression.

By neglecting the importance of the biomechanical constraints on ultra-sound production, experiments designed to study the hormonal or neural bases of ultrasound production fail to control for confounding variables such as locomotion. For example, Dizinno and Whitney (1977) exposed castrated male mice (Mus musculus) to adult females and measured the latency to first detection of ultrasound. They found that these male mice had longer latencies to production of first ultrasound than either controls or castrates injected with testosterone. They conclude that "male androgen levels influenced the production of short latency ultrasounds by male mice" and that the "results are consistent with the courtship function hypothesized for these ultrasonic calls." Of course, castrates are also much slower to investigate a female and attempt intromission. These potential confounds are not considered, however, because ultrasound production is commonly viewed as an unconstrained behavior (Blumberg, 1992).

The possibility that a vocalization is an incidental by-product of locomo-tion, or any other behavior, does not preclude the possibility that the vocalization conveys information that can be used by conspecifics. For example, female receptive behaviors are facilitated by the ultrasonic vocalizations of male ham-sters (Mesocricetus auratus; Floody and Pfaff, 1977). But finding such an effect of a vocalization is not a sufficient demonstration that it has a communicatory function (Blumberg and Alberts, 1992).

The 22-kHz Vocalization of Male Rats

Male rats (Rattus norvegicus) emit this "long call" following ejaculation, during aggressive encounters, as well as spontaneously during the day or night (Barfield and Geyer, 1972; Francis, 1977; Adler and Anisko, 1979). On the basis of contextual correlations, Francis (1977) writes that "it is unlikely that these calls are non-functional because they are so common, because they do not occur randomly, and because they are continually produced even though they could endanger the caller in natural conditions" (p. 238). Similarly, others write that "it occurs with temporal regularity and is very loud... . It would be difficult to accept that a behavior pattern with such an insistent quality would be without communicatory significance" (Barfield et al., 1979, p. 471).

But the search for a communicatory function of the 22-kHz vocalization has not been successful. For example, following the discovery that the vocaliza-tion is emitted by a defeated male after an aggressive encounter, it was suggested that the vocalization serves to inhibit further physical aggression by the dominant rat (Sales, 1972). Despite the finding that the vocalization correlates with aggressive behaviors, it has not yet been demonstrated that the vocalization has any effect on the aggressive behaviors of conspecifics. Similarly, attempts to demonstrate an affect of this vocalization on conspecifics during sexual encoun-ters have not been successful (see Blumberg and Alberts, 1991a).

Failure to identify a role for the 22-kHz vocalization in modulating behavior has spawned additional, new hypotheses. For example, after one unsuccessful attempt to identify a communicatory effect of the 22-kHz vocalization in aggressive behavior, it was concluded that "even if domesticated rats are potentially similar to wild rats in the social regulation of aggressive behavior, they might acquire responsiveness to 22-kHz vocalizations only after they are reared in a more natural environment" (Takeuchi and Kawashima, 1986, p. 550). Similarly, the authors of another paper write that "the failure to demonstrate a role for ultrasonic vocalizations in the present study and [in another] study may reflect the constraints of the experimental procedure and testing conditions employed" (Takahashi et al., 1983, p. 211). They then suggest another communicatory role for the vocalization.

Negative results often generate new hypotheses that can be empirically tested. We see a problem, however, when the accumulation of negative evidence has little effect on the underlying assumption that the vocalization serves a communicatory function. Instead, as illustrated above, investigators explain negative evidence as the result of unspecified variables, termed "unnatural" conditions or inappropriate methods. If such suspicions arise—and they frequently do in studies of natural behavior under controlled and constrained conditions—the investigators may reasonably be expected to specify, if not alter and test, the critical variables. In the absence of specific explanations for unsuccessful experiments, however, it is appropriate to consider explicitly the possibility that the vocal emission does not serve a communicatory function; indeed, that possibility should be the null hypothesis.

Despite widespread treatment in the literature of the communicatory aspects of the rats' ultrasonic vocalizations, we concentrated instead on the physiological bases of this vocalization (Blumberg and Alberts, 1991a). Citing experimental evidence that the vocalization accompanies the increases in oxygen consumption and brain temperature that occur during the "chill phase" of fever (Blumberg and Moltz, 1987), and noting that laryngeal braking accompanies this phase of fever in lambs (Johnson and Andrews, 1990), we hypothesized that the 22-kHz vocalization may, like the vocalizations of infant rats, be the acoustic by-product of laryngeal braking. This hypothesis, although in need of direct testing, is consistent with the fact that the contexts in which this vocalization is emitted involve profound physiological activation (see Blumberg and Alberts, 1991a). Moreover, if supported, this hypothesis directs our attention toward those features that could make it informative to conspecifics. In other words, improved understanding of the physiological correlates of the vocalization will suggest ways in which conspecifics could potentially benefit from the information being provided. On the other hand, as we learn more about the vocalization, we may discover that the information provided is not valuable or not reliable, thus helping to explain the continued lack of success in identifying an effect of the vocalization on receivers.

MORE EXAMPLES OF INCIDENTAL SIGNAL PRODUCTION

Although the vast majority of animal signals have been investigated from the perspective of communicatory function, there have been a number of instances where researchers have attended to mechanism and, by doing so, have enriched our perspective.

Acoustic Signals

The sneezing behaviors of a number of species of New World monkeys have received more than a little attention, and a number of different explanations have been put forth for these behaviors, including roles as display and displacement behaviors, as well as responses to infection. For example, as described above, McLanahan and Green (1977) suggested that the sneeze-like Snough vocalization of golden lion tamarins (Leontopithecus rosalia) "may communicate completion of an activity."

In contrast, and in a beautifully reasoned analysis of this sneezing behavior, Schwartz and Rosenblum (1985) showed that previous explanations of sneezing were insufficient and unsupported, and they provided their own explanation for this behavior following a series of simple but novel experiments. As these investigators raised and lowered the air temperature inside a cage housing a squirrel monkey (Saimiri sciureus), they monitored the occurrence of sneezing. They found that the rate of sneezing increased as air temperature was raised and decreased as air temperature was lowered. Based on these observations, as well as considerations of hemodynamic changes in the head during a sneeze, they hypothesized that sneezing helps to regulate brain temperature during heat stress. Although their hypothesis has not been tested directly, their perspective dramatically alters the conventional approaches of previous investigators, and suggests that these sneezes may not be the controlled communicatory signals that some researchers have assumed.

Gans and Maderson (1973) discuss the many mechanisms underlying the wide variety of reptilian sound production. These authors are particularly sensitive to the incidental nature of many of these sounds, mentioning the faint whistling during expiration in turtles and the sounds accompanying the defensive fecal expulsions of many lizards and snakes. (They write (p. 1197): "Fecal discharge is of course a common defensive mechanism in squamates, but the associated sound is usually much less specific.") Gans and Maderson conclude their review with a passage that reflects on mechanism and historical origins:

> Such [reptilian] sounds might be initially produced by the convulsive expiration of air (the less the pulmonary filling, the greater the flexibility of the trunk). They might occur when portions of the body's keratinous cover are rubbed against each other in an agitated animal. They might,

furthermore, arise when appendages involved in excitement vibrations contact leaves, twigs, or portions of the substratum. All of the patterns actually observed represent (relatively minor) amplifications upon such themes. (p. 1202)

Demski, Gerald, and Popper (1973) review sound production in teleost fish. They note, for example, that fish of various species make sounds while swimming, while grinding their teeth during eating, and when caught and taken out of the water. Fish sounds are also produced by the release of gas bubbles and by the muscular contraction of the swim bladder. Although, for example, the feeding sounds of predators feeding on prey are attractive to other predators and repellent to other prey, these authors state that "many of the sounds produced by fish may have no biological significance but may be incidental to other aspects of the fish's behavior" (p. 1142).

Olfactory Signals

As we have seen, vocal signals can be shaped by natural selection or merely incidental to physiological or biomechanical processes. Similarly, researchers of olfactory communication have struggled with the distinction between those olfactory signals that qualify as pheromones in the strict sense (i.e., involving species-specific chemical release and a well-defined response) and those that are nonspecific chemical signals (Beauchamp et al., 1976).

One attempt to deal with this conceptual distinction between pheromonal and incidental olfactory emission involved the olfactory signals of bullhead catfish (Ictalurus nebulosus; Bryant and Atema, 1987). These researchers were investigating whether catfish use body odors to detect the presence of newcomers to a territory and found that catfish exhibited increased aggression toward another fish fed a "strange" diet. Thus, catfish appear to be sensitive to relatively small changes in the olfactory stimuli in the waste products of other animals, and these stimuli are sufficient to regulate dominance and territorial relationships between these fish. Faced with this striking example of a signal that is an incidental by-product of digestion, Bryant and Atema suggest that "it is possible, perhaps likely, that many so-called pheromones in vertebrates will turn out to be rather nonspecific metabolites, exerting their influence by virtue of chemical habituation and familiarity" (p. 1658). The clear inference from this statement is that students of olfactory communication, like those in acoustic communication, may be invoking relatively complex explanations when more simple ones will suffice.

Galef (1986) similarly argues against the tendency among communication researchers to focus on ritualized or formalized displays and ignore the more subtle ways in which animals learn about their world. In his studies of the means by which weanling Norway rats (Rattus norvegicus) learn what foods to eat, Galef has shown that these young animals use olfactory cues on the breath of

postprandial adults to orient them to nonpoisonous foods. Galef stresses that these breath cues are passively emitted by the adults as incidental by-products of ingestion, thus allowing these animals to adapt to different environments in which the identity of safe foods may vary.

Visual Signals

This form of communication, especially as regards facial expressions, has been the focus of attention before and since Darwin's classic contribution to the subject (Darwin, 1872/1965). Like other areas of communication, there has been a tendency to overinterpret the meaning of facial expressions. Ghiselin (1974) states that investigators of facial expression in humans and primates "tend to presuppose that emotional expressions are there for the sake of communication, ignoring Darwin's view that some have a communicative function and others do not" (p. 255). Although human facial expressions have been reinterpreted within a physiological, homeostatic framework (Zajonc, 1985), the assumption that facial expressions serve primarily as communicatory signals remains because of a lack of direct experimental evidence to the contrary.

Damselflies exhibit a behavior called wingclapping in which the wings are spread apart and then snapped together. Investigators have suggested that this behavior functions as a territorial declaration and/or as a signal between an ovipositing female and her mate that they are both present (Bick and Bick, 1978). Wingclapping, however, occurs in other contexts as well including feeding, grooming, and even when a female is alone (Erickson and Reid, 1989). Erickson and Reid hypothesized that wingclapping by damselflies (Calopteryx maculata) is a thermoregulatory behavior (perhaps by cooling the body surface convectively or through some other mechanism) and, in support of their hypothesis, showed that wingclapping increases during radiant heating.

The dynamics of pigeon (Columba livia) flock behavior provide a striking example of how receivers interpret incidental visual information in their environment. Davis (1975) investigated a phenomenon known as the "contagion of flight," in which an individual bird can induce flight in an entire flock. Others had tried, without success, to identify the "alarm signal" that induces this contagion. Studying this phenomenon in pigeons, Davis observed that under normal conditions these birds typically engaged in preflight behaviors before taking off. When, however, a pigeon took off suddenly and thus did not engage in these preflight behaviors, the other pigeons in the flock took off as well. Thus, it may be the absence of a behavior that induces contagion of flight in pigeons, not the presence of an alarm signal. This example demonstrates once again how receivers can use incidental information provided by conspecifics.

WHAT ABOUT BIRDSONG?

"In the adaptation of birds to an aerial environment, the evolution of feathers and a remarkably efficient respiratory system have incidentally enabled birds to develop complex systems of communication" (Hooker, 1968, p. 311).

As a group, birds emit more complex, rich, and varied vocalizations than do mammals. Related to this difference between avian and mammalian vocalizations, neuroethological approaches to birdsong have paid dividends far exceeding similar approaches in mammals; the notion of a young bird learning the local "dialect" from an adult bird is commonplace in the birdsong literature and is virtually unheard of in the mammalian literature. Functionally, male birds appear to accrue reproductive benefits from singing, although such benefits are admittedly "not well established" (Kroodsma and Byers, 1991). But even as various hypotheses regarding the functional importance of birdsong gain and lose support, we will still be left with the basic, vexing question, "Why birdsong and not, for example, ungulatesong?" Does the answer to this question lie in the ecology of birds, their physiology, or both?

Natural selection works on the components of characters that already exist. One of the initial barriers to acceptance of Darwin's theory was that of explaining the presence of complex and seemingly perfect structures for which intermediate structures were not evident. Understanding the perfection of the eye presented such a problem to Darwin, as did the geometric harmony of the bee's honeycomb. These are no longer considered difficult problems for Darwinism; a simple eye is better than no eye at all, and some exquisitely complex structures emerge from the application of remarkably few behavioral rules (e.g., wasp nests; Kugler and Turvey, 1987). In either case, basic biological materials and behavioral components must exist if natural selection is to have something on which to work.

Understanding acoustic communication in animals requires a similar approach. At the most obvious level, acoustic communicatory systems cannot evolve unless animals can make sounds. Some animals, such as insects, lack an active respiratory system in which air can be expelled through a vibrating structure; instead, crickets, for example, have developed stridulation, in which one wing is rubbed against another (Hoy et al., 1977). Mammals and birds, on the other hand, make noise when they breathe. As Darwin (1872/1965) noted, "Involuntary and purposeless contraction of the muscles of the chest and glottis ...may have first given rise to the emission of vocal sounds" (p. 84). Similarly, Spurway and Haldane (1953) wrote of animal vocalization as "a ritualisation of breathing."

Using the conceptual perspective that we are pursuing here, one might wonder about the physiological bases of birdsong and whether birds have respiratory mechanisms that have been exapted for communication. This perspective is captured by Hooker's statement quoted above, as well as Morris's

(1956) contention that, in birds, "Respiratory changes [have led to] alterations in the breathing rate, amplitude and regularity, which have evolved into vocalisation on the one hand, and inflation displays, on the other." Standing alone, however, these statements do not direct us toward a clear understanding of the evolution of birdsong. Such direction can only be provided by addressing the song production mechanisms of birds directly.

As is well known, birdsong is produced by a novel avian structure, the syrinx, that sits between the bronchi and the trachea. The syrinx (once called the "lower larynx" before Huxley (1877) renamed it, ostensibly to avoid confusion), has become synonymous with the vocal organ of birds. In fact, it was based primarily on syringeal anatomy that Muller, in 1878, first classified the passerine species (Ames, 1971). No doubt, the uniquely structured syrinx of the songbirds, coupled with the uniquely complex songs of these species, have had a profound impact on the nature of experimental investigations of this organ.

The syrinx is very similar in structure to the larynx, although the latter structure is found in both birds and mammals. The larynx consists of membranes controlled by muscles that constrict and adduct the membranes and thus close or open the upper respiratory airway, respectively. Of course, the larynx is recognized as a vocal organ but, as argued in depth by Negus over sixty years ago, several of its functions precede, both in terms of evolutionary time and physiological necessity, the vocal uses of that organ. As Negus (1929) stated it, "in the larynx an organ has been evolved, particularly by arboreal animals, to subserve functions of locomotion, prehension, olfaction and deglutition, and that by the various modifications brought in, an instrument has been provided capable of use for sound production in a highly efficient form" (p. 267). Similarly, the avian larynx serves many functions, including roles in protection against foreign bodies, respiration, swallowing, and modulation of sound (McLelland, 1989).

The syrinx has been treated very differently by comparative anatomists. Its primary role as a vocal organ has apparently never been seriously questioned and, because studies of avian respiration have proceeded without any notice being given to the syrinx, there has never been any reason to doubt that it plays an exclusive role in sound production. Nonetheless, the syrinx, like the larynx, might have evolved as an organ necessary for physiological and/or respiratory regulation and only later was exapted for sound production.

Before addressing this question directly, consider that the avian respiratory system is qualitatively different from that of mammals and must function adequately in environments (i.e., high altitudes) that have very low oxygen concentrations. First, the avian system is unique in that air flows unidirectionally through the bird's respiratory system, in contrast to the mammalian system of bidirectional flow into and out of the lungs (Bretz and Schmidt-Nielsen, 1971). The avian system is also different in that inspiratory and expiratory flow is generated by a series of air sacs. Consider also that passerine species (which have the most highly derived syringeal musculature) maintain metabolic rate and body

temperature significantly higher than do mammals and nonpasserine species (Schmidt-Nielsen, 1984; Caputa, 1984). Moreover, a number of respiratory system mechanisms help protect the avian brain and body from the constant thermal threat posed by elevated body temperatures. These respiratory mechanisms include gular flutter and panting, during which, in some birds, respiratory frequencies can increase 20–30 times over resting values (Dawson, 1982).

We recognize that such discussions of the uniqueness of avian physiology do not bear directly on any possible nonvocal functions of the syrinx. Moreover, we have not found many scientific reports that address this possibility. However, some interesting evidence does exist. Specifically, in a paper devoted primarily to the neural control of sound production in chaffinches (Fringilla coelebs), Nottebohm (1971) reports the consequences of bilateral denervation of the branch of the hypoglossus nerve that innervates the syrinx. He writes:

> An unexpected result of bilateral section of the hypoglossus was the respiratory disorder which overtook the operated birds when placed under respiratory stress. The usual response to respiratory stress, as induced in intact birds by alarm and excess heat, is to hyperventilate... .Seven of the eleven birds died during the first month following the operation. When frightened, they would start producing a "wheezing" sound, drop from their perches, and lie on the floor of their cages. If the disturbance persisted, respiration slowed down and became more laborious until it stopped and the bird apparently died from asphyxia... .[T]he fact that the operated birds do not differ in their behavior from the intact animals as long as they are not disturbed, suggests that their "relaxed" respiratory rhythms are similar. Operated animals, furthermore, keep their weight and general condition well (pp. 235–236).

Nottebohm then provides an explanation for the devastating impact of bilateral denervation of the syrinx:

> During inspiration the soft medial walls, including the internal tympaniform membranes of each bronchus tend to collapse due to the Bernoulli effect... . Thus, when hyperventilation is called for, inspiration becomes more laborious and hypoventilation results. The more frantic the inspiratory effort, the less air reaches the lungs... . If this interpretation is correct, the syringeal musculature plays an active role during the inspiratory effort, so that bronchial walls are kept taut and the passage of air meets the least resistance (p. 236).

Youngren et al. (1974) make a similar observation in chickens (Gallus gallus), a nonpasserine species. These investigators examined the effects of bilateral hypoglossectomy on their birds during exercise. They write: "The hypoglossectomized birds quickly became exhausted, made low wheezing sounds during inspiration and expiration, and recovered very slowly during their exertions. The normal bird was difficult to exhaust, did not wheeze, and recovered almost immediately" (p. 412). Moreover, these same investigators found that activity of one syringeal muscle, the tracheolateralis, is tightly coupled to respiratory activity, again suggesting that at least part of the syringeal anatomy has a nonvocal function. Conversely, they also found that "nearly normal calls can be evoked when both the sternotrachealis and the tracheolateralis muscles are inactivated" (Youngren et al., 1974, p. 412). Clearly, there is room to doubt

the widely held view of the syrinx as an organ with an exclusively vocal function (see also Brackenbury, 1989; Phillips and Peek, 1975).

The evidence just cited is too slim to allow us to draw any conclusions regarding the possible nonvocal functions of the syrinx. On the other hand, the mammalian larynx is an organ that is known to play important roles in respiratory and other physiological functioning and yet, in adult rats, bilateral denervation of either the inferior or superior laryngeal nerves is not a lethal surgical procedure (e.g., Mortola and Piazza, 1987; Thomas et al., 1981). Considering the uniquely complicated respiratory system of birds, perhaps we should not be surprised that denervation of the syrinx is lethal during arousal and respiratory activation. Thus, perhaps the syrinx, like the larynx, is more than simply a vocal organ. If this is indeed the case, the comparative study of avian sound production could be integrated with our substantial knowledge of avian physiology, and, in time, bring us a step closer to birdsong's evolutionary origins.

CONCLUSIONS

> **Desdemona:** Hark! Who is't that knocks?
> **Emilia:** It's the wind.
> —*Shakespeare's Othello* Act IV Scene III

In this chapter, we have argued for greater caution when confronted with a vocalization, or any other signal, about whose production mechanisms we know little. Ignorance of and disinterest in these mechanisms, coupled with the widely held assumption that, a priori, animal vocalizations serve communicatory functions, blurs critical distinctions between the diverse mechanisms that produce these sounds. By blurring these distinctions, we blind ourselves to a signal's information value, its potential for communication, and its evolutionary history. Even more fundamental, however, is that, even in the face of accumulating negative evidence against a signal's design for communication, it is rarely acknowledged that some animal signals have no communicatory function. In sum, increasing attention to the mechanisms that produce and constrain vocal and other communicatory behaviors has the beneficial effect of exposing the historical forces that may have shaped their evolution.

Communication is a dynamic and two-way process, but the current trend of attributing intentionality and other mentalistic categories to a signaling animal (e.g., Hauser and Nelson, 1991) degrades the role of the receiver as an active participant in communicatory systems: *Intention, deception,* and *manipulation* are terms that are nearly always used to describe the sender doing something to the receiver. Furthermore, these terms imply a host of concepts, such as control, planning, and conscious design, that are contrary to the empirical findings of

experimental psychology and inconsistent with our understanding of the serendipity and contrivance of evolution (Blumberg and Wasserman, 1995). The debate over the meaning and applicability of mentalistic concepts as tools for explaining the vocal behaviors of some animals (especially primates) will continue. But such concepts should not become the dominant explanatory tools of animal communication when more parsimonious, less mentalistic, and more empirically fruitful approaches are available.

Given the infinite number of visual, acoustic, and olfactory signals emitted by animals throughout the day and throughout evolutionary history, it is only reasonable to expect that there will be a similar multitude of ways in which animals can interact on the basis of those signals. At one extreme, most signals go unheeded. At the other, some signals are specialized for their communicatory effects and will be received by conspecifics that have specialized detection systems. Between these two extremes, however, lies the diversity that we expect the complexities of animal behavior and the serendipity of the evolutionary process to produce. There are many possible paths from incidental emission to fortuitous effect to communicatory function. Focusing exclusively on communicatory function will only conceal these paths and thus prevent us from unveiling the evolutionary origins of communication.

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