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# Functions and effects in animal communication: reactions to Guilford & Dawkins

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To understand the evolution and diversity of behaviour it is essential to distinguish between functions and effects. This distinction helps to form the critical boundary between a teleological perspective that views animal behaviour as shaped to perfection by adaptive forces and an historical perspective that views animal behaviour as the product of multiple forces, both adaptive and non-adaptive. Teleologists fail to note that the effect of a behaviour pattern may not be identical to its function. In practice, making the distinction is difficult, but strategies have been proposed. For example, Williams (1966) suggested that 'an effect should be assumed 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.'

Guilford & Dawkins (1991) join many other students of animal communicatory signals in making premature proclamations about function. Their analyses and derivations were initially clouded by commission of a classic fallacy, viz., attributing fitness to physical environments rather than to organisms (cf. Pittendrigh 1958). This fallacy can be seen in their assertions that animal signals themselves have attributes such as detectability, discriminability and memorability. These are not qualities of physical stimuli per se, but are properties determined by the sensory, perceptual and neural apparatuses of organisms. It is organisms, not environments, that detect, discriminate and remember information.

Animals continuously emit an uncountable array of messages (signals) that are conveyed as odours, vocalizations, behaviour patterns, colorations, etc. Some of the information contained in these messages is valuable, some is not. But even when a signal (1) does contain important information, (2) is detectable, discriminable and memorable to a receiver, and (3) elicits behavioural responses that are beneficial to the emitter and/or the receiver, there is still no basis for concluding that the signal is adapted for communication. As Gould & Vrba (1982) pointed out, to do so is to confuse current utility with historical origin.

To illustrate this point, consider the human infant with respiratory distress syndrome. A baby with this condition must be kept warm so that its respiratory system is not activated; when cold, these babies increase oxygen consumption and often emit audible grunts. These grunts are acoustic by-products of laryngeal braking, a respiratory manoeuvre that involves laryngeal constriction and expiration against the closed larynx; this manoeuvre helps the infant to maintain lung inflation and arterial oxygenation (Harrison et al. 1968). Although the grunt is an acoustic by-product of a homeostatic mechanism, it is also clearly a signal. In fact, the detection of infant grunting led paediatricians to investigate the underlying respiratory manoeuvre, resulting in medical treatments that mimic the effects of laryngeal braking. Thus, the infant's grunt is a signal that communicates important information, is detectable, discriminable and memorable, and elicits a behavioural response that is beneficial to the sender. On the other hand, this signal is an incidental by-product of laryngeal braking and, therefore, there is no basis for concluding that the grunt is adapted for communication.

Based on a number of physiological similarities, we have hypothesized that the ultrasonic 'distress call' of infant Norway rats, *Rattus norvegicus*, is, like the human infant's grunt, an acoustic by-product of laryngeal braking (Blumberg & Alberts 1990, 1991). This hypothesis also accommodates the notion that the vocalization is part of a communicatory system. In fact, a communicatory role for pup ultrasound is supported by the fact that this vocalization elicits orienting responses and searching behaviour by mothers (Allin & Banks 1972). There is even evidence that the auditory sensitivity of various rodent species has been modified so that two sensitivity peaks are evident, including

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one that corresponds to the vocalization frequency of conspecific young (Brown 1973).

We stress, however, that evidence supporting a communicatory role for pup ultrasound does not indicate that the vocalization is adapted for communication. Rather, we have argued (Blumberg & Alberts 1990) that the vocalization is a non-adapted behaviour pattern that has come to have survival value; in other words, it is an exaptation (Gould & Vrba 1982). This perspective provides a context that highlights how secondary adaptations may have shaped the behaviour and physiology of both pups (e.g. increasing the likelihood of ultrasound emission during laryngeal braking) and mothers (e.g. tuning auditory sensitivity as described above), resulting in a more effective communicatory system. It is important to recognize that senders and receivers can drive evolutionary changes in each other during the formation of a communicatory system (Alberts 1985).

The conventional wisdom regarding rodent ultrasound dictates that pups vocalize because they are experiencing emotional distress (i.e. isolation from the nest) and are therefore motivated to 'call' their mother. The description of these vocalizations, upon their discovery, as 'distress calls' induced by 'isolation' presumes a function for these vocalizations. To avoid such prejudgements of function, our use of language in describing animal signals must remain functionally neutral until clear evidence is available that can distinguish between hypotheses.

Unfortunately, Guilford & Dawkins have added to the teleology that pervades the literature on animal communication. Specifically, they write of 'strategic' and 'tactical' design of communicatory signals, terminology that parallels the more conventional language of ultimate and proximate causation, respectively. The use of such military nomenclature, however, is unfortunate because it suggests that evolutionary forces are similar to military generals designing animals to achieve a particular objective. This underlying teleological perspective is reflected in much of their writing. For example, they write of 'intended receivers' of signals and 'responses sought by the signaller'; elsewhere, they write that 'the particular signal one species employs to achieve this [strategy] may be quite different from the signal another species uses'; they also repeatedly write of 'design for detectability' and 'design for discriminability'. The use of such teleological language can sometimes simplify biological writing, particularly when the philosophical foundation of a field is established. When, however, a field such as animal communication is still searching for such a foundation, teleological language can confuse and distract rather than simplify because it demands and promotes the error of confusing functions and effects. Thus, 'the issue is not whether there is purpose in nature, but whether language will be our slave or our master' (Ghiselin 1969).

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