ANIMAL BEHAVIOUR, 2002, **63**, 397–402
doi:10.1006/anbe.2001.1890, available online at http://www.idealibrary.com on IDEAL®

COMMENTARIES

The discriminating babbler meets the optimal diet hawk

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(Received 2 January 2001; initial acceptance 18 January 2001; final acceptance 1 June 2001; MS. number: AS-1264)

Evidence suggests that some alarm calls function as pursuit-deterrent signals, informing the predator that it has been spotted and it might as well break off the hunt and stop wasting everyone's time (Hasson 1991; Caro 1995). Bergstrom & Lachmann (2001) developed the watchful babbler game to identify the necessary conditions for alarm calls to function as a reliable signalling system between prey and predator. They derived two main results: (1) prey must accurately assess the risk of predation and should call only when the perceived risk is high, and (2) prey that call must be less profitable to the predator (less catchable) and the predator should reject them. My goal is to place this elegant mathematical analysis into its historical conceptual frameworks and show that this opens up useful new insights. It might also make the mathematics more accessible to a broader audience. I think it is useful to understand that what Bergstrom & Lachmann have done is to set a signal detection problem for the prey and a diet choice problem for the predator. Their necessary conditions for a reliable signalling solution can be interpreted to say that (1) the prey must be optimal signal detectors and avoid too many false alarms (Getty 1985; Wiley 1994), while (2) the predators must forage according to the optimal diet algorithm and selectively pursue the more profitable noncalling prey type (Pulliam 1974; Stephens & Krebs 1986). This is a remarkable synthesis of signal detection theory, optimal foraging theory, signalling theory and game theory.

The Discriminating Babbler

I will begin my exposition by explaining why the watchful babbler is a discriminating babbler faced with a signal detection problem. What follows is a redescription of the babbler's strategy in signal detection terminology. Signal detection theory is a Bayesian approach to discriminating discrete quality types ('states of nature'), given continuously variable sensory cues, prior expectations about the state of nature and the expected payoffs to alternative actions. The archetypal signal detection problem involves a person receiving Morse code and having to categorize stimuli of variable length as either short (dots) or long (dashes). Because of noise in the system, some dots are relatively long and some dashes are relatively short. There are two ways of getting this right (guess:state::short:short and long:long) and two ways of getting it wrong (short:long and long:short).

The watchful babbler is faced with a classic signal detection problem. It has to make a binary choice (call/signal, S, or not call/signal, NS) that has four possible outcomes, depending on two probabilistic states of nature (predator present, P, or not present, NP) (see Fig. 1). In signal detection jargon, calling when the predator is not present (S-NP) is a false alarm (FA). The basic problem is why the babbler/prey do not just call all the time (which might be interpreted as superstitious behaviour). False alarms must be costly. Bergstrom & Lachmann (2001) make false alarms costly because they expose the calling babbler to other risks of mortality (c). For instance, calls might attract secondary predators. The probability of surviving a false alarm is $1-c$. Calling in the presence of the predator (S-P) is a hit (H) and it is beneficial because at equilibrium it deters attack by the optimal diet hawk (I will explain why below). The caller is still exposed to secondary predators and the probability of surviving a hit is also $1-c$. Not calling in the absence of the predator (NS-NP) is a correct rejection (CR) and it is not costly because it does not expose the babbler to the secondary predators. The probability of surviving a correct rejection is 1. Not calling in the presence of the predator (NS-P) is a miss (M) and it is costly because the hawk continues hunting and kills the prey with probability $t_x>c$. The probability of surviving a miss is $1-t_x$. I have added the subscript x to Bergstrom & Lachmann's symbol t because the expected payoff is contingent on the cue x (see below).

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