

On the meaning of alarm calls: functional reference in an avian vocal system

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Abstract. Male chickens, *Gallus gallus*, produce qualitatively different alarm calls in response to terrestrial and aerial predators. Field observations suggest that ground alarm calls are evoked principally by animals moving on the substrate, while aerial alarm calls are produced in response to objects moving overhead. In the present study, both types of alarm call were elicited in the laboratory using visual stimuli presented on a video-monitor. Aerial alarm calls were reliably evoked by computer-generated animations simulating a soaring raptor; ground alarm calls were produced in response to a 60-s video recording of a raccoon. Playback experiments were then conducted with six exemplars of each call type, selected to represent the natural acoustic variation in both spectral characteristics and duration. All of the test sessions were videotaped and then analysed, frame-by-frame, by a 'blind' observer. Following playback of aerial alarm calls, hens were significantly more likely to run toward an area of cover than after ground alarm calls or a background noise control. Aerial alarm calls evoked crouching, whereas ground alarm calls caused hens to adopt an erect 'vigilant' posture. Both call types increased the rate of horizontal scanning, but hens were significantly more likely to look upward following presentations of aerial alarm calls. These data demonstrate that chicken alarm calls are functionally referential, encoding sufficient information about the circumstances of production for conspecifics to respond appropriately, even in the absence of contextual cues potentially provided by the non-vocal behaviour of the sender.

Studies of animal alarm calls have proved valuable for addressing both ultimate questions, such as the evolution of signal structure (Marler 1955; Klump & Shalter 1984; Bolles 1988) and proximate ones, such as the way in which visual stimuli are recognized (e.g. Schleidt 1961; Seyfarth & Cheney 1986; Evans et al. 1993). Comparative work on anti-predator behaviour has also revealed considerable diversity in the relationships between signal type, eliciting conditions and receiver response. Some call systems appear principally to provide information about the affective state and the subsequent behaviour of the sender, while others function to designate predator class. Examples of each of these types of call system are provided by research on sciurids and primates, respectively.

California ground squirrels, *Spermophilus beecheyi*, produce structurally-graded alarm calls that form an acoustic continuum from broad-band 'chatters' to tonal 'whistles' (Owings & Virginia 1978). Although 'chatter' calls are usually associated with terrestrial predators and 'whistles' with

approaching raptors, there are clear exceptions to this pattern of usage; whistles are sometimes produced by squirrels that are being chased by carnivores and chatters are elicited by distant hawks (Leger et al. 1980; Owings & Leger 1980). In addition, both call variants also are produced during agonistic interactions with conspecifics (Leger et al. 1980). There is thus a lack of specificity in the circumstances of call production. Consequently, call type has only a probabilistic association with eliciting stimulus. Detailed analyses of call morphology suggest that it also co-varies with the behaviour of the sender (Leger et al. 1980). Consistent with these findings, contextual information plays an important role in determining the response of conspecific receivers (Leger et al. 1979). In reviewing this work, Owings & Hennessy (1984) suggest that variation in ground squirrel call structure principally reflects the differences in response urgency typical of the circumstances under which each call variant is produced.

In contrast, both vervet monkeys, *Cercopithecus aethiops*, (Seyfarth et al. 1980a, b) and ring-tailed lemurs, *Lemur catta* (Macedonia 1990; Pereira & Macedonia 1991) have structurally-distinct alarm

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