The Evolution of Alarm Calling

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INTRODUCTION

Many organisms, particularly birds and mammals, use vocalizations to communicate danger to other members of a group or serve as a warning of a predator. What is still unclear is exactly why these animals give these alarm calls. There are numerous hypotheses that attempt to explain alarm calling: warn other members of the group (Weary and Kramer 1995), let the predator know it has been seen (Blumstein and Armitage 1997, Haftorn 1999, Blumstein 1999), attract attention to the predator (Hogstedt 1983), and to protect close relatives (Hoogland 1983, Taylor et al. 1990) or potential mates (Hogstad 1995). The one factor all alarm calling systems have in common is there is risk involved. It is important that the alarm caller “knows” the cost of calling needs to be outweighed by the benefits gained. The evolution of alarm calls can only occur if the benefits are greater than the costs.

ALARM CALL FUNCTIONS

Even though are multiple functions of alarm calls, the main purpose of alarm calls is to warn other members of a group of danger. Alarm calling seems to be an altruistic event because the caller appears to put itself in danger by attracting the predator’s attention, while leaving time for other group members to seek refuge (Haftorn 1999). These calls may be species-specific, age-specific, sex-specific, or even predator-specific. For example, a female black-tailed prairie dog (Cynomys ludovicianus) more familiar with a territory will be more likely to give an alarm call than a female that is less familiar with a territory (Hoogland 1983). In general, females seem to give alarm calls more
frequently than males (Taylor et al. 1990), and adults are more likely to give alarm calls than juveniles because juveniles would only warn non-descendant kin (Hogstad 1995).

Some alarm calls may be correlated with the distance between the caller and the predator. Calls are more likely to be made when the predator is at a greater distance away. It has been postulated that the distance between the predator and prey may be the most likely measure of risk (Taylor et al. 1990). Alatalo and Helle (1990) studied alarm calling in willow tits (*Parus montanus*) and found that only 10% of the birds gave alarm calls when a simulated hawk was 10 m away, but nearly half of them gave alarm calls when the hawk was 40 m away. This suggests that alarm calls may be given more often when the hawk is too far away to hear the call and the caller can remain unnoticed by the hawk, yet still alarm any nearby relatives. The caller may increase its risk of being noticed by the hawk, but if the caller is alarming conspecifics or a mate then it may be worth it to call.

Alarm calling may also function as mate investment. Willow tits (*Parus montanus*), particularly males, will alarm call if their mate is vulnerable to predation (Haftorn 1999). This is important because it may be difficult to mate again before the next breeding season. Therefore, a male has to balance the cost of exposing himself towards a predator by protecting his mate and the cost of losing a breeding season (Hogstad 1995).

Recent studies have focused on the variation of alarm calls within a species. Yellow-bellied marmots (*Marmota flaviventris*) have three distinct alarm calls: a whistle, a trill, and a chuck (Blumstein and Armitage 1997). Whistles were by far the most common vocalization in this study, but marmots always used the same call for both
terrestrial and aerial predators. Instead, they changed the intensity, or speed, of the same call in relation to the risk. The chuck calls were only produced when the marmot appeared to be disturbed, but not alarmed. Trills seemed to only be used when the threatening stimulus was approaching, making it a “high-risk” vocalization (Blumstein and Armitage 1997). It was also noted that marmots would only make an alarm call if they were within five meters of a burrow (Blumstein et al. 1997). This type of alarm calling system has also been documented in three other marmot species: Olympic (Marmota olympus), hoary (Marmota caligata), and Vancouver Island (Marmota vancouverensis) (Blumstein 1999) as well as eastern chipmunks (Tamias striatus) (Weary and Kramer 1995). However, there were variations in the trill call between the Olympic, hoary, and Vancouver Island marmots. Olympic marmot trills resembled those of yellow-bellied marmots. The hoary marmot and Vancouver Island marmot trills most resembled the grey marmot and steppe marmot (Blumstein 1999). These results suggest that evolution of alarm calling can occur between similar species. In Brants’ whistling rat, calls are either long or short depending on the current risk. Long calls are associated with low-risk situations (slow-moving snake or a distant far-off human) and short calls are associated with high-risk situations (raptors or nearby humans) with the rat fleeing immediately (LeRoux et al. 2001). This function of long and short calls is reversed in the willow tit where long calls are in response to predators and short calls are in response to events that do not elicit real fright (Haftorn 1999.) An example of an organism that actually gives different calls for different predators is the African vervet monkey (Cercopithecus aethiops). These monkeys give different alarm calls for a venomous
snake, an eagle overhead, and an approaching leopard (Gould 1983). This ability for discriminating between alarm calls makes these monkeys highly advanced alarm callers.

**ALARM CALL RESPONSES**

A major variable in regards to alarm calling is the response to a call. When eastern chipmunks hear a call, they may shift their attention from foraging to predator detection (Weary and Kramer 1995). One form of this shift may be the assumption of an alert posture where the chipmunk will assume an upright bipedal position and remain motionless while it surveys its surroundings. Miller et al. (1990) reported that mallard (Anas platyrhynchos) ducklings respond to a mother’s alarm call by immediately ceasing all vocal and locomotor activity. Yellow-bellied marmots also freeze in response to a threatening stimulus, and then direct a call towards the predator (Blumstein and Armitage 1997). Marmots continue to call towards the predator until it was out of sight or, if the predator continued approaching, the marmot retreated to its burrow. It is also thought that willow tits employ this “I see you” principle of warning the predator that it has been seen and that further approach would be useless because the caller is now prepared and ready to flee (Haftorn 1999). It seems that the target of an alarm call (conspecific or predator) does not influence the ultimate payoff because both warning a conspecific and chasing off a predator can increase direct, indirect, and/or inclusive fitness (Blumstein and Armitage 1998.) However, Bergstrom and Lachmann (2001) reported that even if alarm calls are primarily directed to the predator, they may also serve as sexual selection signals, warnings to kin, or signals of status.

There are examples of when alarm calling and the response to these calls are very non-specific. In the willow tit, calls are made very frequently at many moving objects
including ground predators, aerial predators, and even humans and airplanes (Haftorn 1999). The frequency of these calls means that there must be some cost-benefit ratio involved that favors a call even if it is a false alarm. Both males and females will make an alarm call and the general reaction is either to increase vigilance, freeze on the spot, move to another place in the tree, or dive into cover. Another response that the willow tits employed was to have several birds repeat the alarm call at various distances, thus confusing a potential predator (Haftorn 1999).

**ALARM CALL EVOLUTION**

One of the first hypotheses about the ultimate cause of alarm calling was to warn descendant kin (i.e. offspring and grandoffspring) and thus enhance inclusive fitness. However, warning non-descendant kin (i.e., parents, grandparents, and siblings) may be just as important in the evolution of alarm calling (Hoogland 1983). The idea of alarm calling to warn kin may be the only hypothesis that has been verified (Alatalo and Helle 1990). Blumstein et al. (1997) reported that adult female yellow-bellied marmots with pups tended to call more frequently than other age-sex classes; however, it seemed that marmots only cared about their direct fitness and indirect selection only played a minor role. It is thought that marmots may not be able to assess their inclusive fitness, but can determine whether or not they are surrounded by potentially vulnerable relatives before making an alarm call (Blumstein and Armitage 1998). Blumstein and Armitage (1998) believe that the origin of alarm-calling behavior stems from direct fitness, stating that “animals act as if obtaining direct fitness is more important than obtaining indirect fitness.”
Alarm calling systems can be complex and it is difficult to come up with a
generalized model for alarm calling since so many different species exhibit different
behaviors. As stated before, the one factor that all alarm calling systems have in common
is the cost-benefit ratio. As long as the individual is receiving more benefit than the cost
to make the call, it makes evolutionary sense.
LITERATURE CITED


Questions:

1. Why is the “I see you” principle of calling towards predators advantageous?

2. Which age class is more likely to call? Why?

3. Why is the African vervet monkey considered to be an advanced alarm caller?