# Theories for the evolution of alarm calls

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Alarm Call Evolution: Altruism or Kin Selection?

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Introduction

Humans have always been fascinated by animal communication. One important manifestation of animal communication is alarm calls. Alarm calls, even functionally referential alarm calls, can be observed across many different species. Prairie dogs give alarm calls specific even to the shirt color that a nearby human is wearing (Slobodchikoff 2009). Male blue monkeys give alarm calls that are specific to predator type, distance, and location (Murphy et al. 2013). Even African elephants, who have relatively few predators, give alarm calls when they hear the sound of bees (King et al. 2010). But why did these alarm calls, a seemingly altruistic act, evolve in so many different animal groups? How did some get so specific? Sherman lays out six interesting theories of the evolution of alarm calls. Alarm calls could have evolved to divert the attention of the predator, discourage the predator, alert relatives of the caller, help the group which the caller resides in, reduce the later return of the predator, or warn others who will reciprocating at a later time (Sherman 1977). The main findings have suggested that alarm calls have either evolved as an altruistic act, possibly with reciprocity among the group, or as a mechanism to protect kin (Trivers 1971, Sherman 1977). As for functionally referential alarm calls, meaning that the alarm calls encode specific information about the predator, evolution has been suggested as a response to the need for different escape methods from different predators due to the habitat of the group (Furrer and Manser 2009).

Altruism Theory

Although Koenig (1988) points out that there is no commonly accepted definition of altruism in behavioral ecology (Koenig 1988), it can be explained for the purposes of this review as an act that has a cost to the individual and a benefit for others. Reciprocal altruism, which Trivers argues to be present in alarm-calling birds (Trivers 1971), would be a type of altruism which benefits the individual only when another party reciprocates the act toward the first individual (Koenig 1988). Trivers suggests that alarm calling in birds is reciprocal altruism because alarm calling keeps predators from specializing on the location and species of the caller (Trivers 1971). However, Koenig points out that reciprocal altruism is still speculative in birds (Koenig 1988). Furthermore, it is unlikely; if alarm calling is altruistic and natural selection acted on the individual that had the novel gene for alarm calling, the animal would have no increase in fitness, the gene would not spread, and the trait would not evolve (Charnov and Krebs 1975). This being said, if alarm calling is an altruistic behavior, it must have evolved because of some benefit to the caller (Charnov and Krebs 1975). One speculation is that an alarm call could encode the presence of a predator but leave out the location of the predator, thus causing confusion of the dispersal of the flock while the caller knew exactly how to escape the predator (Charnov and Krebs 1975). However, it has been found that male blue monkeys can in fact encode the predator distance and location, thereby giving all immediate information to their conspecifics (Murphy 2013).

Problems arise in this theory when specific species of birds are studied more closely. The alarm calls of one species of jay, the Siberian jay, were closely

analyzed due to the nature of the groups of this species of jay. In this species, the jays live in social groups comprised of one dominant breeding pair, their offspring, and sometimes non-related immigrant birds (Griesser and Ekman 2004). If alarm calling is altruistic in this species, the dominant breeding pair would call whenever a predator is nearby, regardless of whether they were with immigrants or kin (Griesser and Ekman 2004). However, the results showed that females called only during the breeding season while their kin was present, while males called indiscriminately (Griesser and Ekman 2004). This raises further questions about the intentions of males; do they call indiscriminately to selfishly protect future mates or to dilute a predator attack by providing benefits to immigrants in the group to reduce the caller's chance of being attacked? Willow tits also give alarm calls, but Hogstad (1995) suggests that this is a form of mate investment and evolved for this purpose. Males are dominant and breeding pairs last for several years, so if a female dies, especially during the winter, the male partner will likely be unpaired the following breeding season (Hogstad 1995). Adult willow tit males gave alarm calls more frequently when they could see their mates than when they could not; this implies that alarm calling for this species is primarily a form of mate investment (Hogstad 1995). Since the benefit of having a mate the following season is fairly large for a male willow tit, this is not an altruistic act.

Studies regarding animals other than birds suggest that alarm calling is not an altruistic act. Alarm calling would only be categorized as altruistic if the calling was costly to the caller in some way (Koenig 1988). Round-tailed squirrels only give alarm calls when they are already retreating, thus not

endangering themselves (Dunford 1977). Marmots do not reduce their own chances of survival because they rarely call when exposed to predators, and their calls are acoustically difficult to detect by predators (Barash 1975). There is no real threat to either of these species when they give alarm call, thus destroying the option of alarm calling being altruistic. Furthermore, yellow-bellied marmots can identify who produced an alarm call and will ignore calls after many false alarms (Blumstein and Daniel 2004). Although this seems to support the hypothesis for reciprocal altruism since identification of false callers is important for the reciprocity, there are no known cases of which rodents take turns calling.

Kin Selection Theory

The kin selection theory requires that kin be nearby when alarm calls are given for the function of alerting kin of danger. Kin selection is not altruistic because protecting offspring and other kin is a way to protect the future of one’s own genes. The evolution of alarm calls due to kin selection is definitely dependent on the social system of the species. Belding’s ground squirrels have a social system where females generally stay in their natal territory their whole lives and males are polygynous, do not defend any mates or offspring, and emigrate from their natal territory alone, constantly moving after they mate (Sherman 1977). Sherman (1977) found through an extensive observational study that females call frequently when relatives are nearby and do not call at all when they have no living kin; meanwhile, males rarely call. In another study regarding ground squirrels, Dunford (1977) found that males do sometimes call – but this is only when they are juveniles and their mother and siblings are near. Sherman (1977) hypothesized that

the function of alarm calling is nepotism, and that the evolution of this behavior is due to kin selection.

Similar results are found with Gunnison's prairie dogs (Hoogland 1996). Females with kin in the same territory called more often than females who did not have nearby kin. This species has a slightly different social system than Belding's ground squirrels. Males guard 3-4 females and move between adjacent territories, and it was observed that males give alarm calls regardless of whether or not they had kin in the territory (Hoogland 1996). It is likely that the males had kin in adjacent territory, so these kin could theoretically be close enough to benefit from an alarm calls. These prairie dogs assess their own personal safety before calling, as they are more likely to call if they are farther from the danger (Hoogland 1996). Previously it had been found that male Black-tailed prairie dogs only give alarm calls only after they sire offspring in the territory (Hoogland 1983). These studies show extreme support for the hypothesis that alarm calls evolved as a form of selecting for kin.

A study on chipmunk alarm call behavior offers support that there could be a reciprocal altruism component to the maintenance of alarm calling in the species (Smith 1978). This is because they are one of few species in which all members of the group can and do give alarm calls (Smith 1978). Although kin selection was most likely the basis for the evolution of the behavior since older females with many nearby daughters give the most alarm calls (Smith 1978), it is interesting that both seemingly opposing hypotheses can work together.

When yellow-bellied marmots call, the spotted predators almost always leave. However, not all of these marmots call. Blumstein and Armitage (1975) found that the calling is generally a safe activity for these marmots so there is not much cost associated with alarm calls. Their hypothesis is that some individuals do not call because they are trying to reduce reproductive competition (Blumstein and Armitage 1975). Females are the most likely to call, and only when they have vulnerable young. So if another female refrains from calling when she spots a threat, she will reduce the competition for her young since the most vulnerable are the young which are ignorant to the threat (Blumstein and Armitage 1975).

Further Extensions and Conclusions

There are also factors which affect the complexity of alarm calls, including the level of sociality and habitat composition of species. Sociality and communicative complexity were compared across three different sciurid rodents, and only in marmots did communicative complexity increase with sociality; there was no correlation for prairie dogs or squirrels (Blumstein and Armitage 1997). This implies that alarm repertoire size has many factors, such as facial and laryngeal morphology and habitat acoustics (Blumstein and Armitage 1997). Habitat could influence the evolution of functionally referential alarm calls because if different escape routes are needed for different predators due to the physical nature of the habitat, then it would be beneficial to your survival to have different alarm calls for each type of predator to streamline the escape (Furrer and Manser 2009). However, this hypothesis is not completely supported by data. In Gunnison’s prairie dogs, the habitat does influence the alarm calls; they have been found to change

their alarm call dialects for different levels of vegetation cover (Perla and Slobodchikoff 2002). However, meerkats and Cape ground squirrels live in the same habitat yet only meerkats have functionally referential alarm calls; thus habitat does not have a profound influence on the evolution of functionally referential alarm calls (Furrer and Manser 2009). The continuing evolution of alarm calls into more complex communication like functionally referential alarm calls is an important angle of study.

How much of alarm call behavior is learned? Female Campbell's monkeys produce three alarm calls in the wild but only two in captivity, one of which is not observed in the wild (Oattara et al. 2009). This implies that the capacity for alarm calling evolves, but not fully utilized if not needed. This study also suggests that in order for alarm call behavior to be expressed in a population, the threat of predation must be large. Since captive monkeys do not have predators, they have lost vocalizations associated with this danger (Oattara et al. 2009).

The evolution of alarm calls is no simple matter. When factoring in the specific ecology of each species studied to give alarm calls, it all comes down to each species' life history. It makes sense evolutionarily for a species which live in social groups comprised of kin and non-related individuals to call to warn kin, and if only females live near kin, for females to predominantly call. However, if a species lives in a different type of social group, alarm calling does not necessarily have to function as a way to warn kin. Alarm calling in species of many different types of social groups should be studied in regards to the hypotheses offered by Sherman (1977) in order

to find support for other evolutionary drivers as well as reciprocal altruism and kin selection.

Literature Cited

Barash, David P. “ Marmot Alarm-Calling and the Question of Altruistic Behavior.” *American Midland Naturalist* 94. 2 (1975): 468. Print.

Blumstein, Daniel T. “ The Evolution of Functionally Referential Alarm Communication: Multiple Adaptations; Multiple Constraints.” *Evolution of Communication* 3. 2 (1999): 135-47. Print.

Blumstein, Daniel T., and Janice C. Daniel. “ Yellow-bellied Marmots Discriminate between the Alarm Calls of Individuals and Are More Responsive to Calls from Juveniles.” *Animal Behaviour* 68. 6 (2004): 1257-265. Print.

Blumstein, Daniel T., and Kenneth B. Armitage. “ Does Sociality Drive the Evolution of Communicative Complexity? A Comparative Test with Groundâ€ Dwelling Sciurid Alarm Calls.” *The American Naturalist* 150. 2 (1997): 179-200. *JSTOR* . Web. 14 Mar. 2014.

Blumstein, Daniel T., and Kenneth B. Armitage. “ Why Do Yellow-bellied Marmots Call?” Animal Behaviour56 (1998): 1053-055. JSTOR. Web. 1 Mar. 2014.

Charnov, Eric L., and John R. Krebs. “ The Evolution of Alarm Calls: Altruism or Manipulation?” *The American Naturalist* 109. 965 (1975): 107-12. *JSTOR* . Web. 15 Mar. 2014.

Dunford, Christopher. “ Kin Selection for Ground Squirrel Alarm Calls.” *The American Naturalist* 111. 980 (1977): 782. Print.

Furrer, RomanD., and MartaB. Manser. “ The Evolution of Urgencyâ€ Based and Functionally Referential Alarm Calls in Groundâ€ Dwelling Species.” *The American Naturalist* 173. 3 (2009): 400-10. Print.

Griesser, Michael, and Jan Ekman. “ Nepotistic Alarm Calling in the Siberian Jay, Perisoreus Infaustus.” *Animal Behaviour* 67 (2004): 933-39. *Science Direct* . Web. 14 Mar. 2014.

Hogstad, Olav. “ Alarm Calling by Willow Tits, Parus Montanus, as Mate Investment.” *Animal Behaviour* 49. 1 (1995): 221-25. Print.

Hoogland, John L. “ Nepotism and Alarm Calling in the Black-tailed Prairie Dog (Cynomys Ludovicianus).” *Animal Behaviour* 31. 2 (1983): 472-79. Print.

Hoogland, John L. “ Why Do Gunnison’s Prairie Dogs Give Anti-predator Calls?” *Animal Behaviour* 51. 4 (1996): 871-80. Print.

King, Lucy E., Joseph Soltis, Iain Douglas-Hamilton, Anne Savage, and Fritz Vollrath. “ Bee Threat Elicits Alarm Call in African Elephants.” Ed. Karen Mccomb. PLoS ONE5. 4 (2010): E10346. Print.

Koenig, Walter D. “ Reciprocal Altruism in Birds: A Critical Review.” *Ethology and Sociobiology* 9. 2-4 (1988): 73-84. Print.

Murphy, Derek, Stephen E. g. Lea, and Klaus Zuberbühler. “ Male Blue Monkey Alarm Calls Encode Predator Type and Distance.” *Animal Behaviour* 85. 1 (2013): 119-25. Print.

Ouattara, Karim, Klaus Zuberbühler, Eliezer K. N'goran, Jean-Emile Gombert, and Alban Lemasson. " The Alarm Call System of Female Campbell's Monkeys." *Animal Behaviour* 78. 1 (2009): 35-44. Print.

Perla, Bianca S., and C. N. Slobodchikoff. " Habitat Structure and Alarm Call Dialects in Gunnison's Prairie Dog (Cynomys Gunnisoni)." *Behavioral Ecology* 13. 6 (2002): 844-50. *Oxford Journals* . Web. 6 Feb. 2014.

Sherman, P. W. " Nepotism and the Evolution of Alarm Calls." *Science* 197. 4310 (1977): 1246-253. Print.

Slobodchikoff, C. N., Andrea Paseka, and Jennifer L. Verdolin. " Prairie Dog Alarm Calls Encode Labels about Predator Colors." *Animal Cognition* 12. 3 (2009): 435-39. Print.

Smith, Stephen F. " Alarm Calls, Their Origin and Use in Eutamias Sonomae." *Journal of Mammalogy* 59. 4 (1978): 888. Print.

Trivers, Robert L. " The Evolution of Reciprocal Altruism." *The Quarterly Review of Biology* 46. 1 (1971): 35. Print.