

## **Are Marmot Alarm Calls Condition Dependent?**

Austin L. Nash, Alexandra H. M. Jebb and Daniel T. Blumstein

Department of Ecology & Evolutionary Biology, University of Colorado, 265 UCB, Boulder,  
CO 80309, USA

School of Biological Sciences, Zoology Building, Tillydrone Avenue, University of Aberdeen,  
Aberdeen, AB24 2TZ

The Rocky Mountain Biological Laboratory, Box 519 Crested Butte, CO 81224, USA

Department of Ecology and Evolutionary Biology, University of California, 621 Young Drive  
South, Los Angeles, CA 90095-1606, USA

### **Abstract**

The production and structure of animal signals may be condition dependent and may provide more than one type of information to receivers. While alarm calls are not typically viewed as condition dependent, recent studies have suggested that their structure and possibly their propensity to be emitted depends on condition and state. We asked whether the propensity of yellow-bellied marmots (*Marmota flaviventer*) to emit calls is influenced by their immunological or parasite status, by quantifying both trap-elicited and natural calling rates as a function of their neutrophil to lymphocyte (NL) ratio, the presence of a blood borne trypanosome, and the presence of several intestinal parasites (*Eimeria*, *Entamoeba*, and *Ascaris*). We built linear mixed effects models to determine if the health measures we collected were associated with the probability of calling in a trap and with annual rates of wild alarm calling. Marmots infected with trypanosomes were marginally more likely to call when trapped and called naturally at

significantly higher rates. *Ascaris* was negatively associated with the probability of calling when trapped. NL ratio was not directly associated with in trap calling probability, but males were more likely to call when they had higher NL ratios. Thus, internal conditions such as parasite infection and immune system activation can modulate the production of alarm signals and thus provide potential information to both predators and prey about the caller's condition.

Keywords: Alarm Calling, animal communication, condition dependence, parasites, immune response

## Introduction

Animals emit alarm calls in response to detecting a predator in an attempt to escape predation or to warn conspecifics (Caro 2005). However, the propensity to emit calls is a function of multiple factors. Whether an individual emits an alarm call may depend on the presence of other conspecifics or heterospecifics, termed audience effects (Marler and Evans 1996; Ridley, Child, and Bell 2007). For instance, male Thomas's langurs, *Presbytis thomasi*, will only alarm call while fleeing from tigers if other Thomas langurs are present (Wich & Sterck, 2003). The production of calls may also depend on if an individual is in a position of safety (Randall et al. 2000). Great gerbils, *Rhombomys optimus* (Randall et al. 2000), yellow-bellied marmots, *Marmota flaviventer* (Collier et al. 2010), and black-tailed prairie dogs, *Cynomys ludovicianus* (Hoogland 1995), alarm call more frequently when they are near the safety provided by their burrows. The degree of risk an individual is exposed to can also influence whether or not an individual alarm calls and the structure or rate of those calls (Blumstein and Armitage 1997). For instance, marmots are more likely to alarm call to a

predator species that presents high risk, such as coyote, *Canis latrans*, than lower risk predators, such as hawks, and as risk increases they call at higher rates (Blumstein and Armitage 1997). An individual's position in its social network can also affect whether or not it calls and marmots that are socially connected to fewer individuals (less popular) are more likely to alarm call, possibly because they can rely less on other marmots. Secondly, marmots with weaker relationships, which involve fewer interactions between individuals, are more likely to call, possibly to gain social status (Fuong et al. 2015).

In addition to external conditions, internal state, such as stress and parasite load, can affect propensity to call and alarm call structure (Bercovitch, Hauser, and Jones 1995; Blumstein, Patton, and Saltzman 2006; Nouri and Blumstein 2019). Rhesus macaques, *Macaca mulatta*, are more likely to alarm call with higher cortisol levels (Bercovitch, Hauser, and Jones 1995) and marmots are more likely to emit alarm calls when they have higher fecal glucocorticoid levels (Blumstein, Patton, and Saltzman 2006). Furthermore, the acoustic structure of calls can be influenced by condition; marmots with *Eimeria*, an intestinal parasite, produced noisier calls (quantified using Weiner entropy) than those without *Eimeria* (Nouri and Blumstein 2019).

Following on from Nouri & Blumstein's (2019) result, given that parasite status may influence call structure, we ask whether parasites and/or immunological condition can influence the probability that a marmot will emit an alarm call. We quantified this several ways.

Neutrophil to lymphocyte ratio is a measure of stress and innate immune system activation that can be analyzed from blood samples (Davis et al. 2008). Some parasites such as *Eimeria* (Yun et al. 2000) can generate an immune response in hosts while others such as *Ascaris* (Faquim-Mauro and Macedo 1998), *Entamoeba* (Soboslay et al., 2006; Lejeune et al., 2009), and *Trypanosoma* (Hirokawa et al., 1981; Albright et al., 1990) are immunosuppressive. Individuals with activated

immune systems might be less likely to escape or avoid predation due to reduced energetic reserves or reduced energetic investment in vigilance.

It remains an open question as to whether this increased vulnerability influences the propensity to emit alarm calls. It is possible that more vulnerable animals may make themselves less conspicuous (Endler 1987; Hedrick 2007), particularly if calling is costly. Crickets, *Gryllus integer*, who had more conspicuous mating songs behaviorally compensated to this increased predation risk by waiting longer to call after interrupted by predator cues (Hedrick 2007). When predation risk was greatest, guppies, *Poecilia reticulata*, employed a less conspicuous copulation strategy instead of a visual courtship display (Endler 1987). By contrast, increased vulnerability may make an individual more likely to discourage predators from attacking them by emitting calls (Tilson and Norton 1987; Digweed and Rendall 2009; Marler 1955). Songbird mobbing calls are easily localizable, while aerial predator calls are much less conspicuous (Marler 1955). Reduced energetic reserves may also act directly to influence calling. In white-crowned sparrows, immune system activation has been associated with reduced number of song terminal notes (Munoz et al 2010) and parasite infection has been associated with reduced song production (Gilman et al. 2007)

Additionally, parasites may influence an individual's perception of predation risk as a mechanism to increase parasite fitness. In a famous case, laboratory rats infected with the parasite, *Toxoplasma gondii*, perceived less predation risk towards and were sometimes even attracted to cats, *Felis catus*, the parasite's definitive host (Berdy, Webster, and Macdonald 2000). We know from previous studies that marmot antipredator vigilance is associated with parasite status. The immunosuppressive parasites *Ascaris* and *Trypanosoma* have been associated with less time spent vigilant (Chmura et al. 2016).

Thus, it is likely that a marmot's health status could influence the probability of alarm calling by either causing a reduction in calling due to reduced energetic reserves, or an increase in calling due to greater vulnerability and perceived risk (Nouri and Blumstein 2019, Blumstein and Armitage 1997). It is unclear exactly how these health conditions may affect alarm calling, but previous work allows for predictions to be drawn. If immune activation increases perceived risk, then *Eimeria* infection and NL ratio would be associated with an increased probability of alarm calling while *Ascaris*, *Entamoeba*, and *Trypanosoma* would generate the opposite effect. However, *Eimeria* infection rates and overall parasite load have been shown to be positively associated with noisiness in yellow bellied marmot alarm calls (Nouri and Blumstein 2019), while stressed marmots produce calls that are less noisy (Blumstein and Chi, 2012). This result suggests that sick marmots are less able to energetically invest in calls, thus generating noisier calls, and would then be expected to be less likely to alarm call. If immune system activation is reducing available energetic reserves to call, *Eimeria* infection and NL ratio would be associated with a decreased probability of alarm calling, while *Ascaris*, *Entamoeba*, and *Trypanosoma* could positively associate with alarm calling due to greater energy reserves.

We hypothesized that: (1) Neutrophil to Lymphocyte ratio would be positively associated with probability and propensity of alarm calling in yellow-bellied marmots by increasing perceived risk; (2) *Eimeria* infection and gut parasite richness would be positively associated with probability and propensity of alarm calling by increasing vulnerability through reduced energetic reserves; and (3) *Ascaris*, *Entamoeba*, and *Trypanosoma* infection would have a negative association with probability and propensity of alarm calling. By addressing these questions, we will better understand the suite of factors that may or may not influence alarm

calling and thus constrain the ability of individuals, conspecifics, and heterospecifics to benefit from alarm calling.

## Methods

In and around the Rocky Mountain Biological Laboratory (RMBL) ( $38^{\circ} 77' N$ ,  $106^{\circ} 59' W$ ), teams of trained observers have live-trapped and observed free-living yellow-bellied marmots since 1962 (Armitage, 2010; Figure 4). Here we focus on data collected at 11 geographically discrete colony sites from 2003 to 2016 where marmots were observed throughout the active season (April to mid-September) during times of greatest activity (0700 and 1100 h and 1630 and 1900 h MDT).

We trapped marmots to collect blood and fecal samples, to affix permanent ear tags for individual identification (#3 Monel fingerling fish tags— National Band and Tag, Newport, KY), and to mark individuals with Nyanzol fur dye (Albinal Dyestuff Inc., Jersey City, NJ) for identification during behavioral observations. Marmots were trapped in Tomahawk live traps at known burrow entrances approximately every other week between late May (following snowmelt) and mid-September. We recorded in-trap behaviors, which included whether a marmot alarm called, before transferring marmots to a handling bag for processing.

Blood samples were routinely collected when marmots were trapped. We collected up to 3 ml of blood from the femoral vein of marmots (no more than once every other week) that was then stored in a heparin or EDTA tube. Within two hours of collection, we made a thin film blood smear (Chmura et al., 2016), which was then stained using the Hema 3 Stat Pack (Thermo Fisher Scientific, Inc., Waltham, MA, USA). The presence, or absence, of *Trypanosoma lewisi* was based on a systematic examination of a slide for up to 30 min. Immune system activation in

wild vertebrates can be evaluated by Neutrophil to Lymphocyte ratios in blood samples (Davis, Maney, and Maerz 2008). Neutrophil to lymphocyte (NL) ratio was calculated by counting neutrophils, lymphocytes, basophils, and monocytes up to a maximum of 100 cells or for 30 min per slide, whichever came first.

We collected fecal samples from marmots that defecated while in a trap or during subsequent handling and immediately stored these samples in formalin. Fecal samples were analyzed within six months of collection by performing fecal floats using Ova Float™ Zn 118 (zinc sulfate heptahydrate; Butler Animal Health Supply, Dublin, OH, USA). We used up to one sample for each individual, per month. Intestinal parasite richness was calculated by examining wet slides for the presence of *Ascaris* (a nematode), *Eimeria* (a coccidian), and *Entamoeba* (a protozoan) (Lopez et al., 2013), three fecal-orally transmitted parasites (MacNeal, 1904).

Trained observers quantified all bouts of marmot alarm calling and the identity of the caller, when possible, using 15–45x spotting scopes and 10×40 binoculars from 20-150m away (depending on the marmot's degree of habituation). We used these data to calculate annual rates of wild alarm calling where, according to Fuong et al. 2015:

$$\text{Annual rate of alarm calling (wild)} = \frac{\text{No. observed alarm call bouts (of an individual)}}{\text{No. of hours that individual's colony was observed}}$$

\*We restricted our analysis to colonies observed for  $\geq 50$  hours in a given year.

We analyzed both in-trap calling probability and natural rates of alarm calling separately, to examine our hypotheses using complementary lines of evidence. When animals call in a trap we are certain of its precise health status while natural rates of calling are calculated over a season during which time an individual's health status may change. However, natural calling rates occur in the situation in which they have evolved.

We used the lme4 (Bates and Maechler, 2018) and lmerTest (Kuznetsova et al., 2018) packages in R (R Development Core Team, 2009) to fit linear mixed effects models to explain variation in marmot alarm calling. To determine how parasite load and NL ratio influenced in-trap probability of calling, we fitted generalized linear mixed models. Our fixed effects included predator index, age class, colony size, sex, neutrophil to lymphocyte ratio, the presence of *Ascaris* (0,1), the presence of *Eimeria* (0,1), the presence of *Entamoeba* (0,1), the presence of *Trypanosoma* (0,1) and total parasite diversity. We modeled marmot identity and year as random effects to account for repeated observations of individuals within and between years. To determine how parasite load and NL ratio influenced wild rates of calling, we fitted linear mixed models. Our fixed effects included age class, predator index, colony size, sex, neutrophil to lymphocyte ratio, the presence of *Ascaris*, the presence of *Eimeria*, the presence of *Trypanosoma*, the presence of *Entamoeba*, and total parasite diversity. Again, we modeled marmot identity and year as random effects. Some health conditions interact with other individual marmot characteristics, such as age class and parasite prevalence (Lopez, Wey, and Blumstein 2013). To represent these contingencies, we modeled interactions between the health condition being tested and either predator index, colony size, age class, or sex. If none of the fixed effects were significantly associated with the dependent variable, we fitted a new model again without interactions. We fitted the same model again without the health condition in question and subtracted the marginal  $R^2$  without the health condition from the original model marginal  $R^2$  to calculate the marginal  $R^2$  of the health condition in question. We ensured these models were appropriate for the structure of our data by systematically examining residuals.

Research was conducted under research protocol ARC no. 2001-191-01, approved by the University of California at Los Angeles Animal Research Committee on 13 May 2002 and

renewed annually. All marmots were trapped under Colorado Division of Wildlife permits (TR-917).

## Results

Our final dataset contained 5783 trapping events of 611 individuals, 925 annual wild calling rates from 248 individuals, 1907 blood samples from 525 individuals, and 745 fecal samples from 255 individuals from 14 years of observations and trapping. Both in-trap calling probability and rates of wild alarm calling were associated with some health status measures but not with others. Marmots infected with trypanosomes wild-called at significantly higher rates and were marginally more likely to call when trapped ( $P=0.046$ ; Figure 1). Trypanosome presence explained 2.6% of the variation in wild alarm calling. *Eimeria*, *Entamoeba*, and intestinal parasite diversity were not associated with either in-trap calling probability or wild alarm calling rates ( $P > 0.05$ ). *Ascaris* was negatively associated with the probability of calling when trapped ( $P=0.003$ ; Figure 2) but was not associated with wild alarm calling rates, explaining 0.7% of the variation. NL ratio was not directly associated with in-trap calling probability or wild alarm calling rates ( $P > 0.05$ ). However, there was a significant interaction between NL ratio and sex; males were more likely to call when they had higher NL ratios ( $P=0.042$ ; Figure 3). This interaction explains 0.3% of the variation for in-trap calling probability. No other interactions were significantly associated with either in-trap probability or wild rate of calling. Marmot identity, modeled as a random effect, explains upwards of 71% of the variation in alarm calling and most of the variation across all models. There were no annual effects on either calling measure ( $P > 0.05$ ). No other significant relationships were found.

## Discussion

While marmot identity explained most of the variation in alarm calling, some health conditions did affect calling. We found that the effects of immune system activation and parasite presence on the rate of wild calling and probability of in-trap calling were idiosyncratic. Marmots infected with trypanosomes, a known immunosuppressive blood-borne parasite (Hirokawa et al., 1981; Albright et al., 1990), were marginally more likely to call when trapped and called at higher rates in the wild. However, marmots infected with *Ascaris*, another immunosuppressive parasite (Faquim-Mauro and Macedo 1998), were less likely to call when trapped. Additionally, male marmots with greater immune system activation, as measured by NL ratio (Davis, Maney, and Maerz 2008), were more likely to alarm call in trap. NL ratio showed no association with calling while trapped in female marmots or without an interaction with sex. While these results illustrate that the propensity to call may be influenced by internal factors, they do also suggest that specific pathogens may have specific effects, a finding that is consistent with other studies (Hausfaster, Gerhardt, and Klump 1990; Gilman, Blumstein, and Foufopoulos 2007; Nouri and Blumstein 2019).

*Ascaris* infection is associated with a reduction in the probability for an individual marmot to call while infection with trypanosomes leads to an opposite effect even though both parasites are assumed to be immunosuppressive (Hirokawa et al., 1981; Albright et al., 1990; Faquim-Mauro and Macedo 1998), while *Eimeria* and *Entamoeba* have no association with the propensity to call. These contradictory effects suggest that looking at more than just parasite presence and their effects on the immune system could better determine how internal conditions are influencing and individual's perception of the world.

These parasites could vary in their ability to suppress/activate the immune system of their host and could vary in the extent they reduce the energetic reserves of their host. If energetic reserves were limited by parasite infection so that alarm calls were less likely to be produced, we would expect parasite diversity to be negatively associated with alarm call propensity. While parasite diversity was not associated with alarm call propensity, the degree of parasitic infection could affect individual alarm calling. Investigating how parasite load, not just presence or diversity, affects animal signaling is warranted.

NL ratio was positively associated with in-trap alarm calling but only in males. Male marmots have higher glucocorticoid levels than females, thus undergoing higher levels of baseline stress (Smith et al. 2012). These results are supported by female calls being noisier than male calls, as more stressed marmots produce less noisy calls (Blumstein and Yvonne 2012). Immune system activation may act additively on the additional stress that male marmots experience to increased perceived risk and elicit alarm calls.

It is important to note that these condition-dependent effects are modest and these health factors are likely not the main drivers of alarm call propensity and probability. Marmot identity explained most of the variation in wild rates of calling and more variation than all of our fixed effects for in-trap calling. Other factors that vary individually, such as social status (Fuong, Chaparro, and Blumstein 2015) or temperament (Couchoux et al. 2017), play a more substantial role in generating variation in alarm calling propensity and probability. Health factors potentially affecting alarm calling that could be investigated further include metabolic rates, mass, and testosterone levels. Social status and health characteristics could interact through calling. Animals that are compromised in health and broadcast this information through alarm calls could then lose social standing and be less likely to reproduce (Hare and Atkins 2001; Wey and

Blumstein 2007). Nevertheless, these results have a number of exciting implications for receivers.

Most condition dependent vocal signals that have been studied are sexually selected (Fusani et al. 1994; Beani and Dessi-Fulgheri 1995). In the case of alarm calls, information is being broadcast not to a potential sexual partner, but to many different types of receivers, including conspecifics, heterospecifics, and predators. In marmots, alarm calls not only encode a signal of danger but also information on the condition of the caller through call characteristics (Nouri and Blumstein 2019) and the propensity of an individual to alarm call. This additional information could have differing implications depending on the call's receiver. Conspecifics would be interested the accuracy of a predation risk and the reliability of a caller. Health condition information in calls could give recipients more ability to distinguish the risk given a caller's health status or may add confusion about what the true predation risk is. Heterospecifics that eavesdrop may suffer greater predation pressure when a caller population is sick and calling less or lose foraging opportunities if a sick caller population is calling more. Predators may be able to clue in on and target individuals who are of poorer health, or they might be distracted by sick marmots bluffing about their health. Understanding what information is broadcast not only to other conspecifics, but to an entire auditory community offers an exciting new frontier in animal communication.

**Figures**

Figure 1: Trypanosomes and Wild Calling

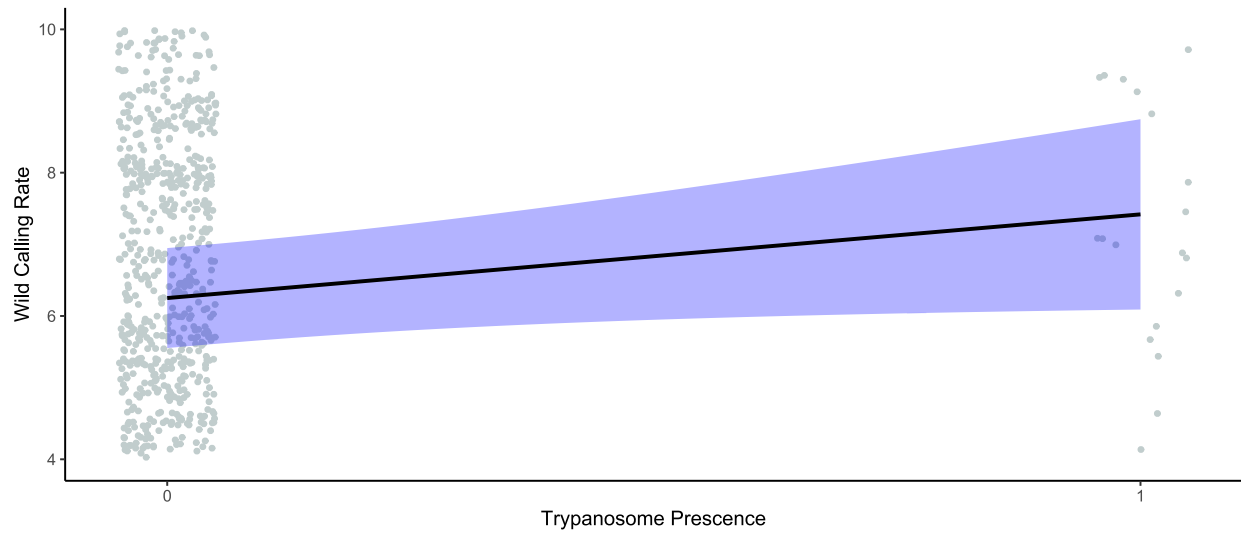


Figure 2: Table of Ascaris and Trap Calling

|              |                 |                |
|--------------|-----------------|----------------|
| Called       | 8               | 106            |
|              | 81              | 550            |
| Did Not Call | 81              | 550            |
|              | Ascaris Present | Ascaris Absent |

Figure 3: Interaction of NL Ratio and Sex

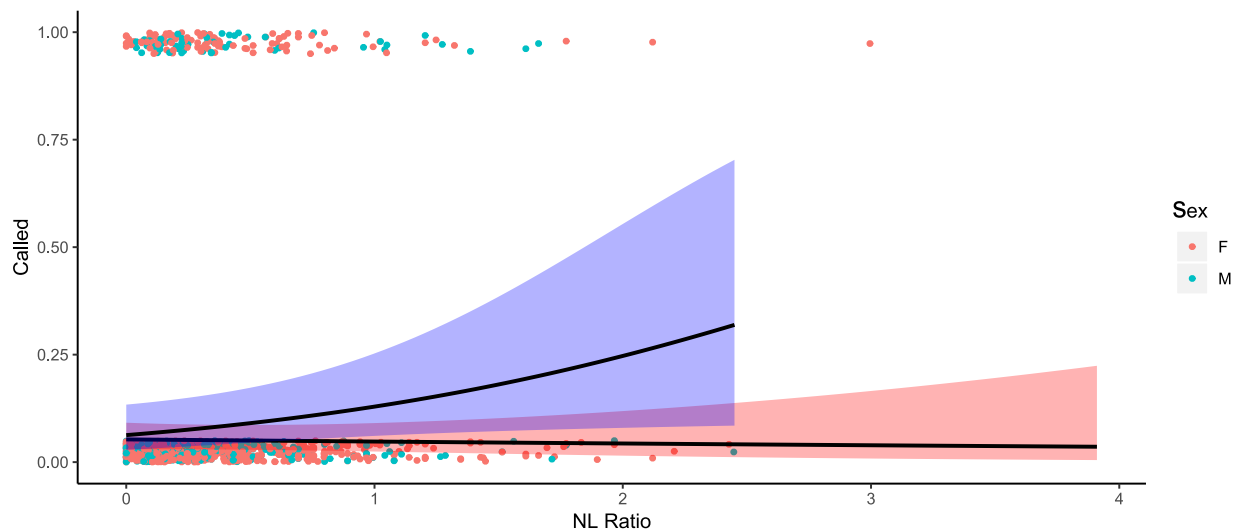


Figure 4: Map of marmot study sites in the East River Valley, Colorado, USA

{Map deleted for size. J.Reithel}

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